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Vol. 17, No. 4 OCTOBER, 1925

PARASITOLOGY

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CAMBRIDGE UNIVERSITY PRESS

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H. K. LEWIS AND CO., LTD., 136, GOWER STREET, LONDON, W.C. 1

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VOLUME XVII OCTOBER, 1925 No. 4

ON THE LIFE HISTORY AND STRUCTURE OF THE EARLY STAGES OF SIMULIIDAE (DIPTERA, NEMATOCERA). PART II.

BY I. M. PURI, M.Sc. (PUNJAB, INDIA), PH.D. (CANTAB.).

(*From the Molteno Institute for Research in Parasitology.*)

(With 15 Text-figures.)

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KEY FOR THE DETERMINATION OF SPECIES OF BRITISH SIMULIIDAE.

Full-grown Larvae.

1. Antennae 4 or 5-segmented 2
Antennae with 9 segments (Text-fig. 19) . . . . . *subexcisum*, Edw.
2. Last abdominal segment rounded ventrally or with a pair of only very small papillae; antennae usually 5-segmented 3

Last abdominal segment with a pair of long conical papillae; antennae 4-segmented . 15
3. Anal gills simple or with a few very short branches 4
Anal gills each with 5 to 10 long branches 11
4. Two basal segments of antennae membranous 5
Two basal segments not membranous but of strong chitin 6
5. Submentum with large bifid teeth (Text-fig. 20) . . . . . *hirtipes* Fries
Submentum with very short simple teeth (Text-fig. 21) . . . *tredecimatum* Edw.
6. Anal sucker with 70 to 85 rows of hooks 7
Anal sucker with 95 or more rows of hooks, markings on the frons-clypeus sharply defined (Text-fig. 18) . . . . . *equinum* L.
7. Frons-clypeus with dark spots arranged in the form of a cross (Text-fig. 7) . . 8
Frons-clypeal markings otherwise 9
8. Dark spots on the frons-clypeus somewhat diffuse, those on the side of the head faint and not extensive . . . . . *ornatum* Mg.
Dark spots on frons-clypeus sharply defined, those on the side dark and very extensive (Text-fig. 8) . . . . . *ornatum* var. *nitidifrons* Edw.
9. Last abdominal segment rounded ventrally . . . . . *nölleri* Fried.
Last abdominal segment with small ventral papillae 10
10. Frons-clypeus with a large rounded black area (*F*, Text-fig. 9) *reptans* var. *galeratum* Edw.
Frons-clypeus with only a dark spot in the posterior border (*A*, Text-fig. 9) . *reptans* L.
11. Frons-clypeal markings of *ornatum*-type (discs dark) 12
Frons-clypeal markings otherwise 13
12. Number of rows of hooks in the posterior sucker up to 85 . . . *variegatum* Mg.
Number of rows 90 or more . . . . . *monticola* Fried.
13. Head all pale, without markings . . . . . *tuberosum* Lundstr.
Head markings of *nölleri*-type (Text-fig. 1) 14
14. Markings on frons-clypeus as in Text-fig. 14, a faint eye-brow . . *morsitans* Edw.
Markings as in Text-fig. 13, eye-brow absent . . . . . *venustum* Say.
15. Antennae short, ventral papillae with broad bases . . . *erythrocephalum* Dg.
Antennae long and slender 16
16. Anal gills branched, dark spots on frons-clypeus not well defined, eye-brow without a dark spot . . . . . *latipes* Mg.
Anal gills simple, eye-brow with an included dark spot 17
17. Frons-clypeus with dark spots somewhat enveloped in a dark cloud and spots *a* and *d* confluent (Text-fig. 17) . . . . . *aureum* Fries
Frons-clypeus with dark spots sharply defined and *a* and *d* separate *angustitarsis* Lundstr.

Pupae.

1. Prothoracic respiratory organs in the form of thin-walled tubes the main branches of which form a ring on the thorax, rows of spines absent on abdominal segments *equinum* L.
Respiratory organs consisting of a number of slender filaments 2
2. Respiratory filaments eight 3
,, ,, six 8
,, ,, four 13
,, ,, eleven or more 15
3. Upper two pairs of filaments, widely divergent from the lower two, have long vertical stalks, well-developed rows of spines on abdominal segments 5–9 dorsally, cocoon with an anterior dorsal process . . . . . *yerburyi* Edw.
Respiratory filaments otherwise, cocoon without anterior dorsal projection . . 4
4. Filaments arranged in four shortly-stalked pairs 5
Filaments not in pairs, all rather widely divergent, a pair of strong hooks ventrally on abdominal segment 4, cocoon loosely woven . . . . . *nölleri* Fried.
5. A pair of spines present at the posterior end of abdomen, thoracic trichomes simple . 6
Terminal spines absent or as tubercles, thoracic trichomes may be branched, the four lower filaments arise from a common stalk (Text-fig. 14) . . . *morsitans* Edw.

6 Thoracic trichomes long, filaments much shorter than pupa, cocoon with "windows" on each side anteriorly (Text-fig. 9) . . . *reptans* L. and var. *galeratum* Edw.
Thoracic trichomes short no hooks ventrally on abdominal segment 4, filaments about as long as the pupa, cocoon without windows 7
7. Stalks of the two lower pairs of filaments usually longer than those of the upper pairs *ornatum* Mg.
All four pairs of filaments with short stalks of about equal length *ornatum* var. *nitidifrons* Edw.
8. Well-developed rows of spines dorsally on abdominal segments 5 to 9, upper pair of filaments with a long vertical stalk widely divergent from the two lower pairs, cocoon with a long anterior process (Text-fig. 19) . . . . *subexcisum* Edw.
Rows of spines not well developed, filaments otherwise, cocoon without an anterior process 9
9. Filaments somewhat divergent 10
Filaments not divergent 11
10. Terminal pair of hooks and the ventral pair on abdominal segment 4 absent, filaments arranged in sessile pairs (Text-fig. 15) . . . . . *erythrocephalum* Dg.
Both pairs of hooks present, filaments arranged in stalked pairs (Text-fig. 13) *venustum* Say
11. Thoracic trichomes branched, upper pair of filaments considerably thicker than the lower pairs (Text-fig. 10) . . . . . *monticola* Fried.
Trichomes simple, filaments more or less equal in thickness 12
12. A pair of rounded tubercles present on the thorax, cocoon loosely woven anteriorly and much longer than pupa (Text-fig. 11) . . . . . *variegatum* Dg.
Pair of tubercles absent, cocoon throughout closely woven and shorter than pupa *tuberosum* Lundstr.
13. Filaments arranged in two distinctly stalked pairs, cocoon with a long anterior process (Text-fig. 16) . . . . . *latipes* Mg.
Filaments all arising from a common base or nearly so 14
14. Filaments very stout at the base, cocoon with a short anterior process *angustitarsis* Lundstr.
Filaments of equal thickness throughout, cocoon without an anterior process *aureum* Fries
15. Respiratory filaments 14 (11 to 14), terminal pair of hooks absent, cocoon closely woven . . . . . *tredecimatum* Edw.
Filaments 16 or 50 and over, terminal pair of hooks present, cocoon loosely woven shapeless mass (Text-fig. 20) . . . . . *hirtipes* Fries

MORPHOLOGY OF LARVAE AND PUPAE.

N.B. The descriptions of *Larvae* apply throughout to *full-grown* specimens except where otherwise stated (see pp. 351, 354).

Where in the descriptions species are compared the comparison only applies to the corresponding stages of development.

Measurements of length followed by breadth are given thus 3·7 × 1·3 mm.

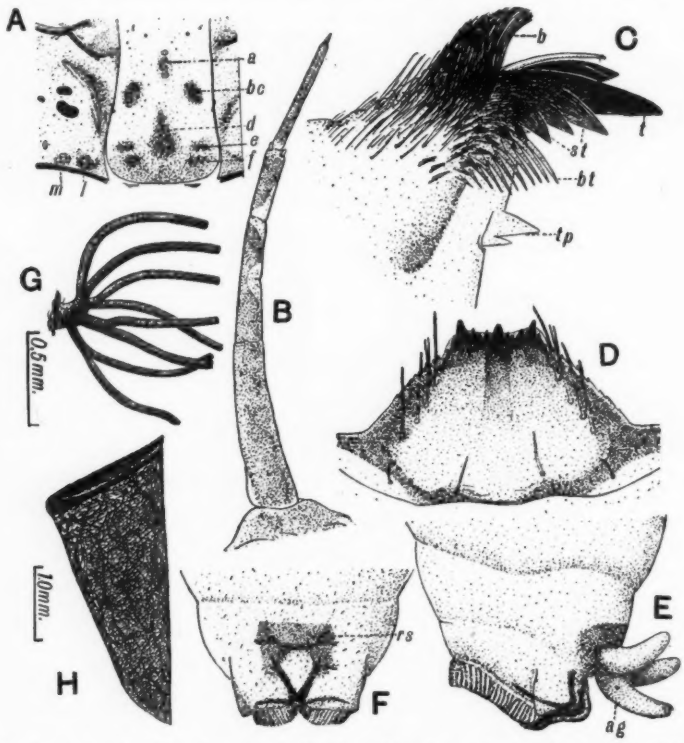
All figures of the corresponding parts of larvae and pupae of different species are drawn to the same scale, except *H*, Text-fig. 16 (which is only half the normal scale) and the figures of the *head-capsules*.

In all figures of the highly magnified *respiratory filaments of the pupa* the basal portion only is shown (examples *G*, Text-fig. 7; *B*, Text-fig. 8; etc.) except in *S. equinum* (*G*, Text-fig. 18).

(2) I. **SIMULIUM ORNATUM** Meigen, 1818.

LARVA.

Average length 7·6 mm.[1] Body-colour variable, usually greenish-grey. *Head* (*A*, Text-fig. 7) yellowish-brown, lighter than in *S. nölleri*, but the groups of discs much darker and form the nucleus of dark spots. Spot *a* is



Text-fig. 7. *S. ornatum* Mg. LARVA. *A*, Portion of head-capsule showing head markings. *B*, Right antenna, ×152. *C*, End of mandible (right) from ventral side, ×440. *D*, Dorsal view of submentum, ×152. *E*, Side view of posterior end. *F*, Dorsal view of posterior end. PUPA. *G*, Respiratory filaments of right side. *H*, Lateral view of cocoon.

a–f, *l* and *m*, groups of discs; *a g*, anal gills; *b*, cluster of bristles; *b t*, bristle-like teeth; *r s*, rectal scales; *s t*, three light-coloured teeth; *t*, terminal teeth; *t p*, teeth-like processes.

faint, *b* and *c* are dark and coalescent, *d* is large and wedge-shaped, and *e* and *f* are faint, *e* often obscure. The lateral head-spots *l* and *m* are faint. Above and in front of the eyes is a dark stripe with a slightly darker sub-median spot, and below the eyes are two faint round patches. In larvae from

[1] Average length of French larvae 8·8 mm.

Palestine, Salonica and France the spots *l* and *m* are darker than in larvae from Great Britain, being much like those of *S. ornatum* var. *nitidifrons*, and in some cases even darker and more extensive.

Antennae (*B*), comparatively longer than in *S. nölleri*, 5-segmented, division between 2nd and 3rd segments very faint. Basal segment a little shorter than 2nd and 3rd together, 3rd about half as long as 2nd, which sometimes appears faintly divided into two in the middle, 4th about as long as 2nd. *Cephalic fan-filaments* number 45–50. *Mandibles* (*C*). The row of teeth *b t* consists of 10 or 11 teeth, with a row of 5–7 teeth behind these, more or less continuous with teeth *s t*. *Submentum* (*D*) has 9 teeth in front row, median tooth and the one at each end much enlarged and the 3rd tooth from each side the smallest in the row. Below the submentum, on each side there is a row of 4–6 long hairs in British larvae but of 5–8 in those from the Continent.

Anal gills three, simple (*E*). *Rectal scales* (*r s*) darker, more numerous and extend much more on the sides than in *S. nölleri*. At the posterior end there are two very small ventral papillae, with broad bases. These papillae are better developed in the larvae from the Continent than in the British ones, in which they are distinguishable only in specimens with fully extended posterior ends. *Posterior sucker* with 79–85 rows, each row having 11–15 hooks.

Chaetotaxy of head and body about the same as in *S. nölleri* except that hairs behind and ventral to spiracular scars in the latter are absent.

PUPA.

Size: British specimens average 3·7 × 1·3 mm., French 4·6 × 1·5 mm. Sensory hairs, hooks and spines as in *S. nölleri*, except that spines on 9th segment are generally very small and the pair of strong ventral spines on 4th segment are absent.

Respiratory filaments (*G*) about as long as pupa, eight in number[1] and arranged in shortly-stalked pairs. The stalks vary much in length but those of the two lower pairs are usually longest. The ventral pair is slightly thinner than the others. All the filaments lie more or less in the vertical plane and the ventral-most invariably curves backwards, very often under the pupa.

Cocoon about 3·9 × 1·8 mm., covering the pupa more or less completely. It is dark brown in colour, tough and closely woven (*H*). There are no windows or spaces in the web and the anterior margin is thickened into a strong rim. There is no floor in the anterior half of the cocoon.

Material collected: Larvae in company with those of *S. ornatum* var. *nitidifrons*, *S. reptans*, *S. monticola* and *S. latipes* from a small stream with stony bed near Polperro, Cornwall (A. W. R. Roberts, 17 June, 1923).

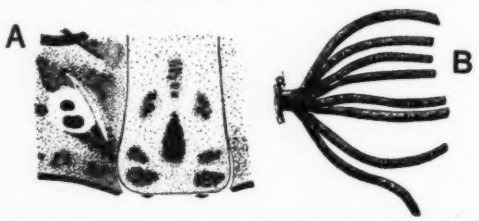
[1] I have come across only two cases of variations in the respiratory filaments. In the one, on the left side, besides the usual 8, there was a short stumpy filament arising from the stalk of the 2nd pair from the top, while in the other case, the stalk of the uppermost pair was very long and the two filaments below it arose separately from this stalk.

France: Larvae and pupae in large numbers with those of *S. aureum* from Erguy, Côtes-du-Nord (M. Langeron). Large numbers of pupae on blades of grass in R. Moselle (near Maxeville), Meurthe and Moselle (E. Séguy). Larvae from R. Arentéle near Brouvelieures, Lower Vosges (E. Hubault, Summer, 1922). Larvae and pupae from a stream near Valence (L. Léger, Sept. 1924). Innumerable larvae and pupae in company with those of *S. aureum* from Vallée Heureuse, Marquise near Wimereux (D. Keilin, 2 Sept. 1924). Larvae and pupae with a few of those of *S. aureum* and *S. latipes* on submerged grass blades in small streams of the fortifications of Grenoble (24 Sept. 1924). Larvae in company with those of *S. equinum* from R. Mortagne, Barrage de Mont (in January), and from a spring at Bouxières-aux-Dames (in March, 1925) both near Nancy (E. Hubault).

(2) II. **SIMULIUM ORNATUM** var. **NITIDIFRONS** (Edwards), 1920.

LARVA.

The dark spots on frons-clypeus as in *A. ornatum* but comparatively larger and darker. A large dark spot behind, and another somewhat lighter in front of the eyes. Black spot in the eye-brow much more pronounced (*A*, Text-fig. 8). *Cephalic fan-filaments* number 40–44 and *posterior sucker* has 72–76 rows with 11–15 hooks per row.



Text-fig. 8. *S. ornatum* var. *nitidifrons* Edw. *A*, Portion of larval head-capsule showing head markings. *B*, Pupal respiratory filaments of right side.

PUPA.

Like that of *S. ornatum*, except that the pairs of *respiratory filaments* are almost sessile or with very short stalks of about equal length (*B*). All the filaments are about equal in diameter.

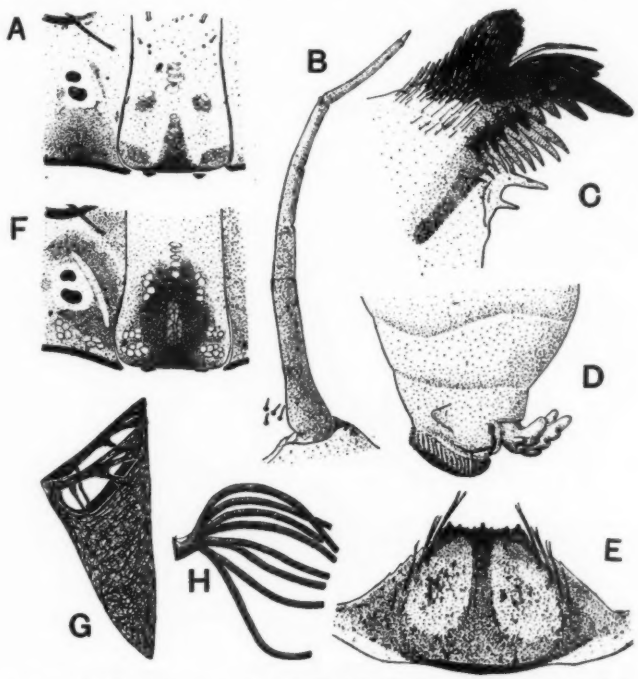
Material collected: Larvae, in company with those of *S. ornatum* Mg. *S. reptans* L., *S. monticola* Fried. and of *S. latipes* Mg. from a small stream with stony bed near Polperro, Cornwall, 17 June, 1923. A few larvae from a small stream in Woody Bay, North Devon, 6 June, 1923 (Both by A. W. R. Roberts).

(3) I. **SIMULIUM REPTANS** Linn. 1758.

LARVA.

Average length 5·5 mm. Body-colour greyish, with conspicuous dark, brownish-grey or greenish bands on the abdomen. *Head* (*A*, Text-fig. 9) light golden or yellowish in colour, with very few pigment spots. A dark spot of

varying size in the middle of posterior margin of the clypeus, often extending into a part of group *d*, when *b c* and *e f* are also faintly pigmented, *a* is not clearly seen. Eye-brow absent but a large dark spot behind the eyes completely surrounds *l* and *m*. *Antennae* (*B*) 5-segmented, division between 2nd and 3rd segments faint. Basal segment about equal to or shorter than 2nd and 3rd together, 2nd about twice as long as 3rd, and faintly divided into two in the middle, 4th about 1½ times as long as 3rd. Basal segment slightly dilated near its base, beyond which the antenna tapers gradually to the end



Text-fig. 9. *S. reptans* L. LARVA. *A–C*, as in Text-fig. 7. *D*, Lateral view of posterior end. *E*, Dorsal view of submentum. *F*, Portion of head-capsule of *S. reptans* var. *galeratum* Edw. showing head markings. PUPA. *G*, and *H*, as in Text-fig. 7.

of 4th segment. *Cephalic fan-filaments* number 47–51. *Mandibles* (*C*). Row *b t* has 8–10 teeth, behind which is another row of 4–6 teeth in continuation of teeth *s t*. Processes *t p* long and placed apart. *Submentum* (*E*) very much darker as compared to the rest of the head-capsule and the appendages, with 9 teeth in the front row and 2 on each side laterally. The teeth in the front row are short with broad bases and as they suddenly narrow down to a point they appear more or less trifid. Ventrally there are 3–5 hairs on each side, 4th and 5th when present, always small. Hairs, especially anterior ones, generally bifid.

Three *anal gills* (*D*) each with 3 or 4 very short branches. This species shows a great variation in the branching of its gills, depending most probably on its habitat. Sometimes the gills are more or less simple with only one or two nodules near their bases, while, according to Roubaud (1907), larvae living in the Tropical Congo have gills with many branches and richly supplied with tracheoles like those in the larva of *S. damnosum*, which is found exclusively in the Tropics. *Rectal scales* as in *S. ornatum* but fewer and dark. Ventro-laterally at the posterior end is a pair of small *papillae* with broad bases. *Posterior sucker* with 78–80 rows with 12–16 hooks per row.

PUPA.

Size 3·0 × 1·1 mm. *Trichomes* simple, comparatively about 1½ times as long as in *S. nölleri*. Cuticular hooks and spines as in *S. ornatum* but sometimes a sensory hair on 4th abdominal segment ventrally becomes strongly chitinised and appears like a small spine. Ends of ventral spines subdivided into 3 or 4 parts.

Respiratory filaments: Eight on each side, about 1·5 mm. long, arranged in 4 short-stalked pairs, the uppermost pair rather shorter than the others (*H*). All the filaments more or less in one plane (vertical) and of equal diameter.

Cocoon (*G*) like that of *S. ornatum* except that on each side at the anterior end is a large open space, crossed transversely by one or two bands of silk. Cocoon is not so tough as in *S. ornatum* and generally has a lighter colour. Floor very incomplete, formed of loose network lying only in posterior half of cocoon.

Material collected: A few larvae from Polperro, Cornwall (A. W. R. Roberts, 17 June, 1923).

(3) II. **SIMULIUM REPTANS** var. **GALERATUM** Edwards, 1921.

LARVA.

Head brownish-yellow. A black spot in the middle of posterior margin of frons-clypeus (*F*, Text-fig. 9), connected anteriorly with a large dark spot surrounding group *d*. Groups of discs unpigmented except *d* which is faintly coloured. A faint eye-brow present connected to a pigment spot behind and another in front of eyes. In some larvae the head is more strongly pigmented than in others, in such cases the lateral wall is pigmented practically all over leaving only a bright halo round the eyes. *Antennae*, 5-segmented, 1st segment about equal to 2nd and 3rd together, 3rd about equal to 2nd, which is not divided into two parts; and 4th is a little smaller than the 1st. *Cephalic fan-filaments* number 48–53. *Submentum* as in *S. reptans* except that in some larvae the end tooth of each side in the front row is not trifid.

Anal gills have small 1–4 nodule-like branches, which are sometimes so small that gills appear simple. *Posterior sucker* with 65–70 rows with 10–14 hooks per row. A small papilla on each side near the posterior end placed more ventrally than in *S. reptans*.

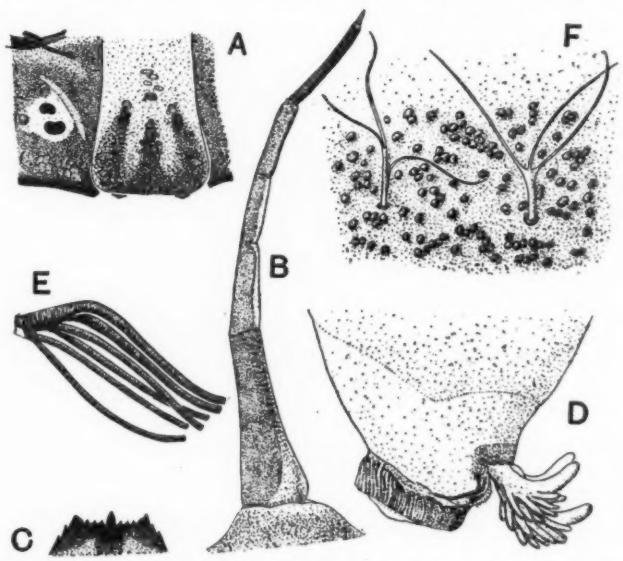
Material collected: One larva (with *S. venustum* Say, *S. morsitans* Edw., *S. tredecimatum* Edw., *S. lyra* Lundstr., *S. pusillum* Fries and a few other spp.) from Tännforsen Falls, Sweden (F. W. Edwards, 15 Aug. 1923).

(4) **SIMULIUM MONTICOLA** Friederichs, 1920.

= *S. obreptans* Edwards, MS.

LARVA.

Average length 7·8 mm. Body-colour greenish-grey with faint bands on first 4 or 5 abdominal segments. *Head* (*A*, Text-fig. 10) dark brown except on dorsal surface, which is golden brown. Posterior border of frons-clypeus dark with a deep black spot in the middle and in contact with discs *d* which are also pigmented. From groups *e* and *f* a streak of pigment (sometimes faint) spreads anteriorly up to discs *b c*, forming a trident-like spot on the head. Laterally the head is very dark with a bright space around the eyes. Eye-brows



Text-fig. 10. *S. monticola* Fried. LARVA. *A* and *B* as in Text-fig. 7. *C*, Distal end of submentum. *D*, Side view of posterior end. PUPA. *E*, Respiratory filaments of right side. *F*, Portion of thoracic wall showing tubercles and "trichomes."

generally have a black sub-median spot. *Antennae* (*B*) 5-segmented, much as in *S. ornatum* except that the base is slightly dilated. *Cephalic fan-filaments* number 36–46, not 29–39 as counted by Friederichs (1921). (In two cases the number of filaments in the right and left fans varied in the same individual—R 45–L 44; R 36–L 37.)

Mandibles. There are 12–14 teeth in row *b t*, with another row of 8 or 9 teeth behind. Processes *t p* and cluster of bristles *b* behind the terminal teeth are

as in *S. tuberosum* (*C*, Text-fig. 13). *Submentum* (*C*, Text-fig. 10) is like that of *S. reptans* except that the median tooth and the one at each end do not appear trifid, and the former is comparatively longer. There are 8–10 long hairs on each side ventrally.

Lateral plates on thoracic proleg strongly chitinised.

Anal gills (*D*) have 8–10 branches each. *Rectal scales* as in *S. ornatum* but more numerous. Number of rows in *posterior sucker* 95–110, each row having 13–18 hooks. No *ventral papillae* at the posterior end.

PUPA.

Average size 3·9 × 1·5 mm. Colour deep brown. *Trichomes* on the head simple, but nearly all on the dorsal surface of the thorax are branched (*F*, Text-fig. 10). Hairs, hooks and spines on the abdomen as in *S. nölleri* except that hairs on 2nd segment dorsally are much stronger and curved forwards to act as hooks, and the pair of ventral spines on 4th segment absent.

Respiratory filaments (*E*) about 2·6 mm. long, 6 on each side, arranged in 3 short-stalked pairs, all running more or less together in the vertical plane. The pairs decrease in thickness from above downwards, the uppermost being slightly swollen near the base.

Cocoon about 4·3 mm. × 1·8 mm., like that of *S. nölleri*.

Material collected: Larvae in company with other species, from Polperro, Cornwall (A. W. R. Roberts, 17 June, 1923). *France.* A number of larvae and one pupa, with larvae of *Liponeura* (Blepheroceridae) from a very fast stream in the regions of *Cols de la Schlucht* and *du Bonhomme*, the higher Vosges, in Summer and Autumn 1924, and again in April, 1925 (E. Hubault). Larvae in company with *S. hirtipes*, from R. "La Vanage," near Servance (Le Magny-Maubert) (P. Remy, 9 April, 1925).

(5) **SIMULIUM VARIEGATUM** Meigen, 1818.

LARVA.

Average length 7·0 mm. Colour of head brownish or dark grey. *Head* markings resemble those of *S. monticola* but are much lighter laterally, the head is often very little pigmented and the eye-brow, spots *l* and *m* and one spot behind and a little above the eyes only are present. *Antennae* as in *S. monticola*, 1st segment a little longer than 2nd, which is sometimes obscurely divided into two parts and is longer than twice the length of the 3rd. *Cephalic fan-filaments* number 46–49. *Mandibles* as in *S. monticola* except that row *b t* has only 9–11 teeth. *Submentum* resembles that of *S. monticola* and has 6–9 long hairs ventrally.

Lateral chitinous plates on thoracic proleg strongly chitinised.

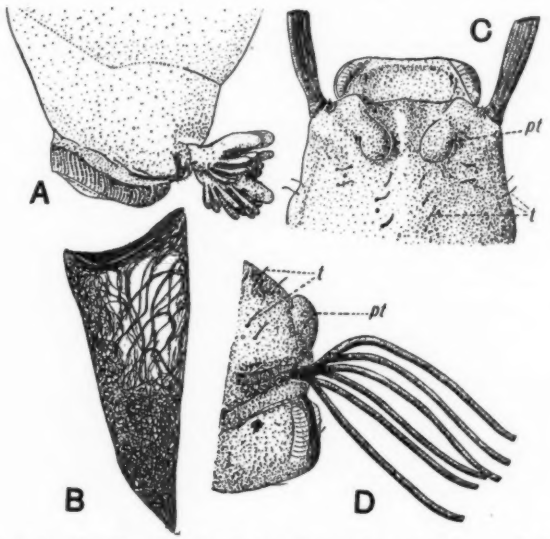
Anal gills (*A*, Text-fig. 11) have each 6 to 9 rather long branches. *Rectal scales* smaller than in *S. nölleri* and composed of a row of 3–8 small spines.

Rows in *posterior sucker* 78–85, each row with 12–15 hooks. No *ventral papillae* at the posterior end.

PUPA.

Average size 3·4 × 1·3 mm. *Trichomes* simple, about 1½ times as long as in *S. nölleri*. Sensory hairs on 2nd abdominal segment dorsally, often curved forwards and strongly chitinised to serve as hooks. Cuticular ventral spines on 4th segment absent, but one or two sensory hairs may sometimes be strongly chitinised and curved.

A pair of hollow, rounded protuberances arise from the dorsal side of the pupa, a little internal and posterior to the origin of respiratory filaments



Text-fig. 11. *S. variegatum* Mg. *A*, Lateral view of posterior end of larva. *B*, Lateral view of cocoon. *C*, Dorsal view of anterior end of pupa showing "Patagia." *D*, Lateral view of the same.

pt, patagia; *t*, trichomes.

(Text-fig. 11, *C*, *D*). These backwardly directed processes (*pt*), are characteristic of the pupae of this species, but there is no structure corresponding to them in the imago.

In many adult insects protuberances of a somewhat similar structure and position have been described as "*Patagia*" by a number of writers and Cholodkovsky (1886), who found them in the adults of many families of Lepidoptera, led by the presence of blood and trachea in these processes, was of opinion that they represent the pair of prothoracic wings of extinct insects. He also said that the prothoracic horns of the pupae of Diptera are homologous to these protuberances in the adult insects. The presence in the pupae of only one species of Simuliidae, of both the prothoracic horns (the respiratory

filaments) and the pair of protuberances, which correspond in structure and position to the *patagia* of adult insects clearly shows that the *patagia*, as already pointed out by Hasse (1886) are merely secondary structures and that it is not, as Cholodkovsky thought, a case of *atavism*.

Respiratory filaments (*D*) about as long as pupa, six on each side and arranged in three short-stalked pairs. All the filaments lie more or less in the same vertical plane.

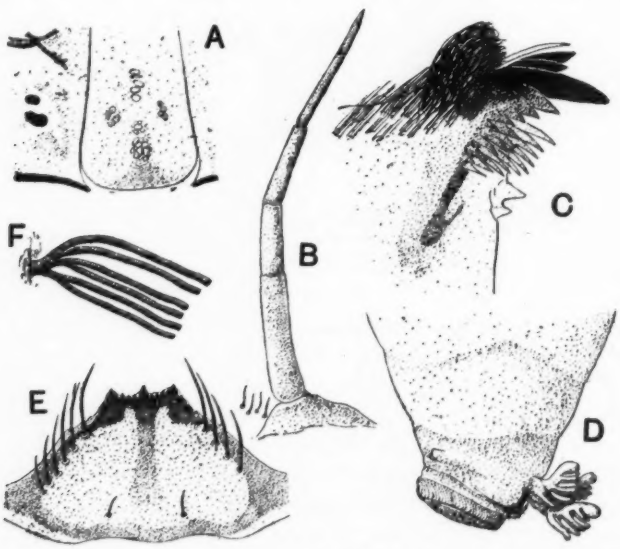
Cocoon (*B*) very large, size about 4·5 × 1·7 mm. Closely woven above and behind but on each side in the anterior half, the network is very open, leaving large spaces. Sometimes the anterior part is very loosely woven and encloses the filaments, at times even closing the mouth of the cocoon.

Material collected. France: Larvae and pupae with *S. venustum* Say, from l'Eau-d'Olle near Allemont, Bourg d'Oisans, Dauphiné (L. Léger, August, 1909).

(6) SIMULIUM TUBEROSUM Lundström, 1912.

LARVA.

Average length 5·7 mm. *Head* very light golden brown with practically no spots. Body-segments 1–5 have dark bands but the posterior segments are all dark dorsally. *Antennae* (*B*, Text-fig. 12) 5-segmented. Basal segment about as long as 2nd and 3rd together, 3rd equal to or a little longer than 2nd,



Text-fig. 12. *S. tuberosum* Lundstr. LARVA. *A*, Portion of head-capsule. *B*, Right antenna. *C*, Terminal portion of right mandible from ventral side. *D*, Lateral view of posterior end. *E*, Dorsal view of submentum. PUPA. *F*, Respiratory filaments of right side.

which does not show any division into two parts, and 4th a little smaller than the 1st. *Cephalic fan-filaments* number 44–50. *Mandibles* (*C*) 5 or 6 teeth behind row *b t*, which has about 8 or 9 teeth. 2 or 3 small teeth usually present in continuation with row *s t*. Processes *t p* are as shown in the figure. *Submentum* (*E*) has 9 teeth in front row. Central tooth and the one at each end considerably longer than others. There are 4–6 long hairs on each side ventrally.

Anal gills (*D*) have about 5–8 branches each. Only a few *rectal scales* lying in groups of twos or threes. Rows in *posterior sucker* 71–75, each row with 11–15 hooks. No *ventral papillae* at the posterior end.

PUPA.

Average size 3·2 × 1·1 mm. *Trichomes*, hooks and spines as in *S. nölleri*, except that a few cuticular spines are present along the anterior border of segments 5 and 6 dorsally, and ventral spines on segment 4 are a little smaller.

Respiratory filaments (*F*) about as long as pupa, six on each side, arranged in three short-stalked pairs which are equal in thickness and are all directed nearly straight forwards and a little downwards, without spreading. The lower two pairs seem to be given off from the main stem which continues as the uppermost pair.

Cocoon like that of *S. ornatum* but much smaller than the pupa (about 2·7 × 1·5 mm.) rarely extending beyond the middle of thorax.

(7) SIMULIUM VENUSTUM Say, 1828.

= *S. austeni* Edwards, 1915.

LARVA.

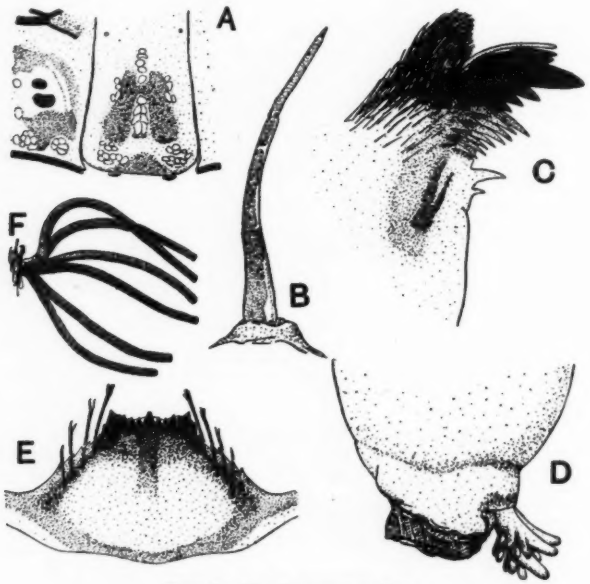
Average length 5·8 mm. *Head* (*A*, Text-fig. 13) light brown. Groups of discs not pigmented. Dorsally there is a pair of large oval dark spots, one on each side of group *d*, connected anteriorly with each other (between *a* and *d*) by a transverse bar of pigment. Usually there is another dark spot along the posterior border of the frons-clypeus. Laterally a faint eye-brow connects a dark area behind the eyes, to another in front. *Antennae* (*B*) 4-segmented, basal segment a little smaller than the 2nd, 3rd about as long as 1st, and 4th is minute. *Cephalic fan-filaments* number 48–55. *Mandibles* (*C*) with 6–8 teeth in row *b t* behind which 4 or 5 teeth form another row continuous with teeth *s t*. Position and size of processes *t p* very variable. *Submentum* (*E*) 9 teeth in terminal row, the middle tooth long and the one at each end of the row very broad. All teeth have broad bases and consequently appear comparatively short. On each side there are 4 or 5 long hairs ventrally, all of which have generally partite ends.

Anal gills (*D*) have each 4–6 adequal branches. Number of rows in the *posterior sucker* 70–75, with 9–15 hooks per row. There are very small *ventral papillae* with broad bases.

PUPA.

Average size 3·7 × 1·1 mm. *Trichomes*, hooks, and spines as in *S. nölleri*.

Respiratory filaments (*F*) slightly longer than half the length of pupa; six on each side, arranged in three short-stalked pairs. Stalk of upper pair slightly longer and thinner than that of the middle, and that of lower pair thinnest and generally longest of the three. Stalk of middle pair generally appears slightly swollen. All the filaments are in the vertical plane near the base.



Text-fig. 13. *S. venustum* Say.
Lettering as in Text-fig. 12.

Cocoon: average size 4·1 × 1·7 mm., like that of *S. ornatum*.

Material collected. *Sweden*: Large number of larvae, with *S. morsitans* Edw., *S. tredecimatum* Edw. and other spp. from Tännforsen Falls (F. W. Edwards, 15 Aug. 1923).

France: Larvae and pupae with *S. variegatum* Mg. from l'Eau-d'Olle, near Allemont, Bourg d'Oisans, Dauphiné (L. Léger, Aug. 1909).

(8) **SIMULIUM MORSITANS** Edwards, 1915.

LARVA.

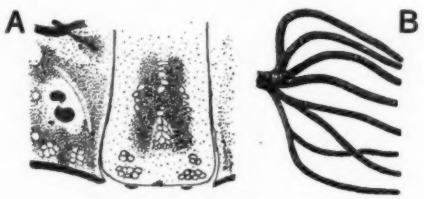
Average length 6·5 mm. *Head* (*A*, Text-fig. 14) golden brown. Groups of discs unpigmented. Frons-clypeus with a well-defined, H-shaped dark median spot. On the head laterally is a dark spot in front and another behind the eyes. A faint eye-brow is usually present. *Antennae* as in *S. venustum* but

the 2nd segment is about 1½ times as long as the 1st, and 3rd is a little smaller than 2nd. *Cephalic fans* and *mandibles* as in *S. venustum* and so is also the *submentum* except that the black terminal portion along the front row of teeth is not so broad as in the latter.

Anal gills and *rectal scales* as in *S. venustum*. Rows in *posterior sucker* 69–75, with 10–15 hooks per row.

PUPA.

Size about 3·5 × 1·2 mm. There are very few minute disc-like tubercles on the head and thorax. Of the thoracic *trichomes* one or two may be bifid. Hooks and cuticular spines as in *S. nölleri* but the dorsal rows are not well developed, those in the terminal segment are very few and faint and the *terminal spines* are reduced to mere protuberances.



Text-fig. 14. *S. morsitans* Edw.
Lettering and scale as in Text-fig. 8.

Respiratory filaments (*B*) about 2·2 mm. long, 8 on each side, arranged in four pairs. Upper three pairs are much like those in *S. venustum* and the lowermost pair arises from the stalk of the third pair. The stalk of the 2nd pair from the top is very small and the filaments appear to arise from the main stem, while that of the lowermost pair is the longest and thinnest.

Cocoon about 3·7 × 1·5 mm. and like that of *S. ornatum*.

In addition to the respiratory filaments, the pupa can be distinguished from that of *S. ornatum* by the presence of a pair of well-developed ventral spines on segment 4, the absence of the terminal pair of spines, the poorly developed rows of dorsal abdominal spines and the presence of very few tubercles on the thorax.

Material collected. Sweden: One larva with *S. venustum* Say, and other spp. from Tännforsen Falls (F. W. Edwards, 15 Aug. 1923).

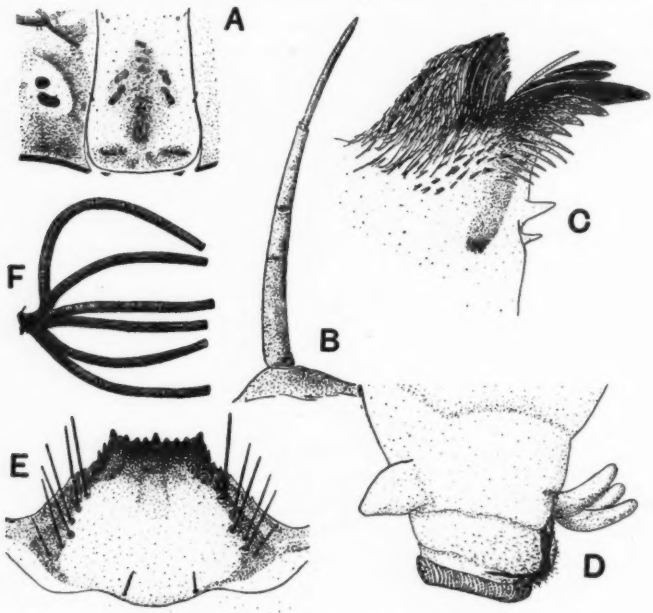
(9) SIMULIUM ERYTHROCEPHALUM[1] De Geer, 1776.

LARVA.

Average length of Spring larvae 7·4 mm. and of Autumn larvae 5·7 mm. while larvae reared from eggs in the laboratory were only 4·1–4·8 mm. long.

[1] This species was described by Edwards (1921) under the name *S. argyreatum* Meigen, but in a letter, addressed to me dated 5 Oct. 1923, he writes: "My studies of the type collection this year shows that it will be necessary to change the name of what we call '*argyreatum* Mg.' to '*erythrocephalum* Deg.' Meigen's type is another species, but De Geer's (30 specimens in good condition) is the same as our summer form of *argyreatum*."

Colour varies from light grey or greenish-grey to reddish-grey, with more or less conspicuous bands on abdominal segments 1–4. *Head* light brown, groups of discs on the frons-clypeus pigmented and appearing as dark spots more or less enveloped in a dark cloud. Groups *b* and *c* separate, *d* darker in the posterior region and *e* not clearly seen. Laterally *l* and *m* are indistinguishable, and an eye-brow is present without any included dark spot. *Antennae* (*B*, Text-fig. 15) 4-segmented, 1st segment a little shorter than 2nd and about equal to 3rd, and 4th is minute. There is a great variation in the relative length of 2nd and 3rd segments of the antenna and in some cases the latter is much longer than the former. The 2nd segment is equivalent to the 2nd and



Text-fig. 15. *S. erythrocephalum* De G.
Lettering as in Text-fig. 12.

3rd segments together of the antenna of *S. ornatum*, but it does not show any division into 2 or 3 segments. *Cephalic fan-filaments* vary very greatly in number; in spring larvae they number 52–54, in larvae reared in the laboratory in August, 38–44, and Friederichs found only 36–38 in larvae from Germany. *Mandibles* (*C*). 6–8 teeth in the row *b t* and only small spinous projections behind them. *Submentum* (*E*) has 9 teeth in the terminal row and 2 small ones on each side, but very often, one of the 2 side-teeth, shifts forwards and comes to lie in the front row which accounts for the 11 teeth mentioned by Edwards. The median tooth, and the fourth on each side of it, are longer than the others. Sometimes the number of teeth in the terminal row is

reduced by the fusion of two teeth on one or both sides. There are on each side 5 or 6 long hairs ventrally.

Lateral chitinous plates on thoracic proleg are as in *S. nölleri* but the projections from their anterior borders are not arranged in groups, as in the latter.

Anal gills (*D*) simple but those in the larvae[1] reared from eggs (under artificial conditions) have 4 or 5 adequal branches. Rectal scales very light in colour. Rows in *posterior sucker* 80–86 with 12–16 hooks per row.

Chaetotaxy. Each segment bears but one pair of long sensory hairs on each side but the number of microsetae, which are tripartite, is very large. The group of prothoracic *pleural setae* differs from that in *S. nölleri* in having an extremely small seta arising just above the pair of long ones.

Early larval stages.

1st stage. 0·6–0·9 mm. long. *Cephalic fans* have 14–16 filaments and hooks in *posterior sucker* are arranged in three concentric rows, each row with 36 hooks. The larva moults after 4 or 5 days.

2nd stage. About 1·3 mm. long. *Head* shows very faint spots. *Frons-clypeus* has become broad as in a full-grown larva. *Antennae* 3-segmented; 1st segment about as long as 2nd, and the 3rd is minute. The two conical processes are at the distal end of 1st segment. *Cephalic fans* have 17–24 filaments. *Mouth-parts* are very much as in a full-grown larva except that the number of cuticular setae is very small. *Submentum* has below it two hairs on each side. *Anal gills* show slight nodule-like protuberances. There are two rows of rectal scales. Number of radial rows on *posterior sucker* 45–52, each row having 4 or 5 hooks. The larva moults after 4–7 days.

3rd stage. About 2·7 mm. long. *Head* shows the dark spots distributed as in a full-grown larva but they are not very conspicuous and the cloud around them is still very light. *Antennae* 4-segmented; 1st segment much longer than 2nd, 3rd a little smaller than 1st and 2nd together, and the 4th is minute. *Cephalic fans* have 21–30 filaments. *Submentum* still only with a pair of hairs below it. *Anal gills* have 3 or 4 small branches each; and the number of rows in the *posterior sucker* is 55–65.

Larva moults after 4–8 days.

4th stage. About 3·7 mm. long. *Head* markings as in a full-grown larva. The 2nd segment of the *antenna* is still small; *cephalic fans* have 30–35 filaments; *submentum* has 3 hairs on each side; and the *posterior sucker* has 64–73 rows of hooks.

Larva moults after 5–8 days.

5th stage. About 4·5 mm. long. The *cephalic fan-filaments* number 35–38 and the *posterior sucker* has 70–77 rows. Larva moults after 5–10 days and passes into the last stage larva.

The larval life from egg to pupa lasts from 4–5 weeks.

[1] The adults, both male and female, reared from these larvae were identified by Mr Edwards as those of *S. erythrocephalum* De Geer.

PUPA.

Average size 3·4 × 1·2 mm. *Trichomes*, hooks and spines as in *S. nölleri*, except that the sensory hairs on 2nd abdominal segment dorsally are strongly chitinised, occasionally a few spines are also present on segment 6, the row on the terminal segment much better developed, and the terminal spines and ventral pair on 4th segment are absent.

Respiratory filaments (*F*, Text-fig. 15) about 2·6 mm. long, 6 in number, roughly arranged in three pairs, the upper and lower pairs have short stalks but the middle pair arises directly from the main stem. The filaments all spread out near their bases, the uppermost nearly vertical.

Cocoon about 3·5 × 1·5 mm., and is like that of *S. ornatum*. It is generally broadest a little behind the anterior end.

(10) **SIMULIUM LATIPES** Meigen, 1804 and 1818.

LARVA.

Average length 6·7 mm. *Head* golden or dark brown, with groups of discs dark but not sharply defined. On frons-clypeus group *d* is darkest and *e* and *f* are enveloped in a dark cloud. Side of the head has a dark area in front and another behind the eyes, both connected by a faint eye-brow, without an included dark spot (*A*, Text-fig. 16). *Antennae* (*B*) long and slender, 4-segmented; 1st segment about 6 times as long as broad, 2nd about $1\frac{1}{3}$ as long as the 1st, 3rd about $\frac{1}{2}$ as broad and $\frac{1}{2}$ as long as 2nd, and 4th is minute. *Cephalic fan-filaments* number 45–55. On the *mandibles* (*C*) the cluster of bristles behind the terminal teeth has a characteristic shape and the proximal of the two processes *t p* is reduced to one or two small narrow projections. *Submentum* (*E*) has 9 teeth in terminal row, the 3rd from each side being the smallest. Sometimes one of the pair of lateral teeth is produced forwards and comes to lie in the terminal row of teeth (thus making 11 in the front row). There are 3–5 long hairs on each side below the submentum.

Friederichs has described two types of larvae of *S. latipes* Mg. from two different parts of Germany. In one type the projections below the teeth of the submentum have serrated edges, while in the other these edges are smooth. In none of the specimens collected from many different parts of England have I found the projections serrated.

Anal gills (*D*) each with 4–6 branches decreasing in size distally. *Rectal scales* simple and few in number. *Posterior sucker* has 75–85 rows, with 10–15 hooks in each. *Ventral papillae* long and conical.

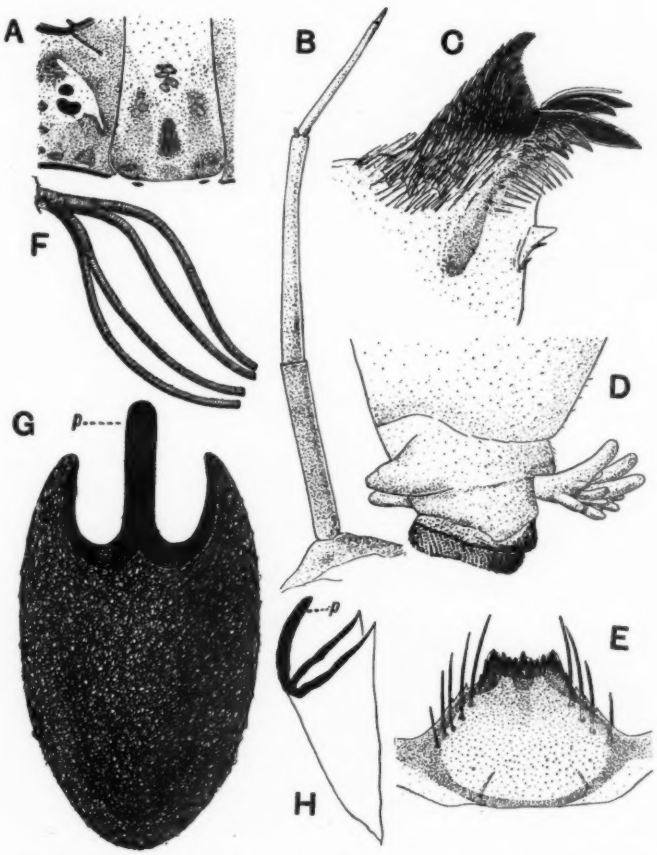
Chaetotaxy. Sensory hairs and microsetae as in *S. nölleri* but comparatively much longer, in some cases being about twice as long.

PUPA.

Average size 4·1 × 1·5 mm. Thoracic *trichomes* very long, sometimes thrice as long as in *S. nölleri* or even longer. Rows of cuticular spines present dorsally on abdominal segments 6–9, a few spines present even on segment 5.

Ventral cuticular spines absent on 4th segment but a sensory hair strongly chitinised and even bifid present in some pupae.

Respiratory filaments (*F*) very long (about 4·8 mm.), 4 in number, arranged in two distinctly stalked pairs. All filaments of about equal thickness and lie in the same plane (vertical) bent down near their bases.



Text-fig. 16. *S. latipes* Mg. *A–F*, as in Text-fig. 12. *G*, Dorsal view of cocoon. *H*, Lateral view of same (scale about half that in *G*).
p, Anterior process of the cocoon.

Cocoon (*G* and *H*) dark brown, tough and closely woven; average size (without the process) 4·8 × 3·1 mm. and usually widest near the anterior end. Anterior border strongly thickened and produced forwards into a long (about 1·3 mm.) flat process (*p*). Floor present only in posterior half and extending dorsally around the abdomen of the pupa. The cocoon is not double as

described by Friederichs, but the floor instead of being attached near the base as in the other species, extends upwards on each side and is fixed along the dorsal wall of the cocoon.

Material collected: Number of larvae with *S. ornatum*, *S. ornatum* var. *nitidifrons*, *S. reptans* and of *S. monticola* from a small stream with a stony bed near Polperro, Cornwall (A. W. R. Roberts, 17 June, 1923). *France*: A few larvae and one pupa from the streams of the fortifications of Grenoble (Sept. 1924).

(11) SIMULIUM AUREUM Fries, 1824.

LARVA.

Average length 7·2 mm. Body-colour pale with reddish or brownish-yellow pigment distributed dorsally. First 4 or 5 segments show obscure bands incomplete ventrally. Groups of discs on the *head* are pigmented, appearing as six dark spots dorsally and five laterally. Dorsal spots sometimes surrounded by a dark cloud and groups *a* and *d* may appear continuous. Eye-brow present with a dark spot which is sometimes almost black (*A*, Text-fig. 17). Lightly chitinised area in the ventral wall of head does not extend beyond the two dark apodemes in the posterior border. *Antennae* (*B*) long and slender, 4-segmented with 1st segment slightly swollen near the base. 1st segment a little smaller or equal to 2nd, which is about one and one-third as long as 3rd; and 4th is minute. *Cephalic fan-filaments* number 48–64. In some larvae the number varies in right and left fans. *Mandibles* (*C*). In row *s t* the central tooth is shortest. There are 8–10 teeth in the row *b t* and behind them is a row of 5 or 6 very small teeth lying close together. Processes *t p* have a characteristic form as seen in the figure *C*. *Submentum* (*D* and *E*) with 9 teeth in front row. Of the pair of lateral teeth the anterior one enlarged and at times appears to lie in front row. In addition to the flat projections of the border of head-capsule below the teeth of the submentum, there is a lamellar process with a serrated border, lying just below the enlarged tooth at each end of the terminal row (*E*). There are 4 or 5 long hairs on each side below the submentum.

Anal gills simple. *Ventral papillae* large and conical. Rows in the *posterior sucker* 70–80 with 10–15 hooks in each.

Early larval stages.

1st stage. Resembles that of *S. nölleri* except in the number of *cephalic fan-filaments*, which in this species is 18–20, and also in the presence of a pair of *ventral papillae* at the posterior end.

2nd stage. 2·2 mm. long; *cephalic fan-filaments* number 21–25; and the number of rows in the *posterior sucker* is 40–46.

3rd stage. 2·9 mm. long; filaments in *cephalic fans* 29–35; rows in *posterior sucker* 51–55.

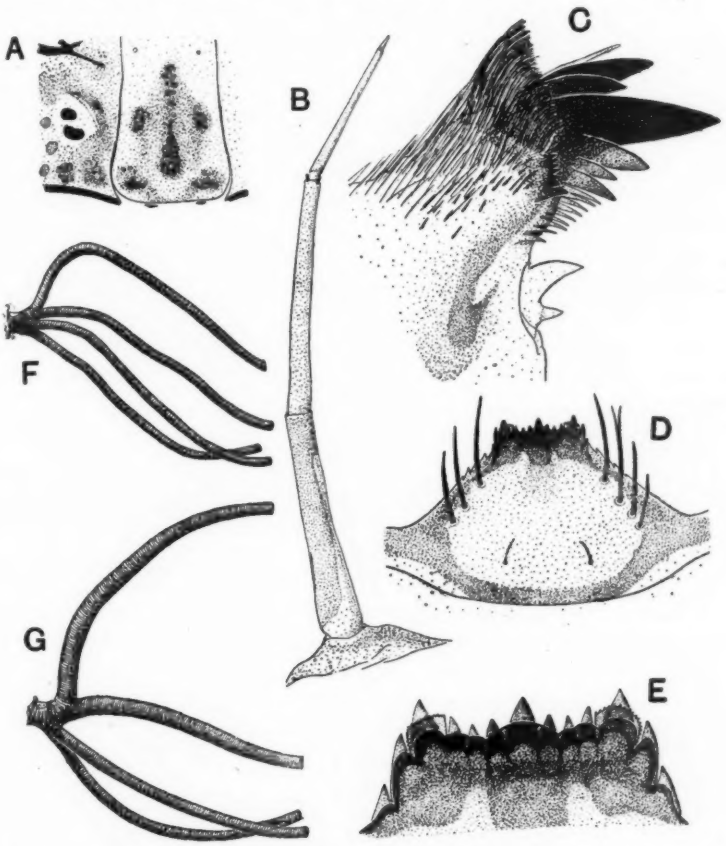
4th stage. 4·5 mm. long; filaments in *cephalic fans* 40–44; rows in *posterior sucker* 58–64.

5th stage. 5·0 mm. long; filaments in *cephalic fans* 44–50; rows in *posterior sucker* 66–73.

The complete larval life lasts 4 to 5 weeks.

PUPA.

Average size 3·4 × 1·2 mm. *Trichomes* simple, about 1½ times as long as in *S. nōlleri*; rows of dorsal cuticular spines present on segments 6, 7, and 8,



Text-fig. 17. *S. aureum* Fries. *A–D*, as in Text-fig. 7. *E*, End of submentum. ×440. *F*, Respiratory filaments of right side. *G*, *S. angustitarsis* Lundstr. Pupal respiratory filaments of right side.

but those on segment 9 extremely minute. *Terminal spines* present. Ventral spines as in *S. nōlleri*.

Respiratory filaments (*F*) about 4·5 mm. long, 4 in number, all arising more or less from the same place. All of about equal thickness, and practically in the same plane (vertical), but do not bend downwards suddenly as in *S. latipes*.

Cocoon: Average size 3·8 × 2·2 mm., as in *S. latipes* but not so tough and has no median anterior process.

Material collected. England: Large number of larvae and pupae from R. Cam near Hauxton. *France*: Larvae and pupae with *S. ornatum* Mg. from Erguy, Côtes-du-Nord (M. Langeron). Pupae from R. Yonne near Sens, Yonne (M. Séguy). Larvae and pupae with *S. ornatum*, from Vallée Heureuse, Marquise, near Wimereux (D. Keilin, 2 Sept. 1924). A few larvae with larvae and pupae of *S. ornatum* on submerged grass blades in small streams of the fortifications of Grenoble (24 Sep. 1924). A few larvae from a spring at Bouxières-aux-Dames, near Nancy (E. Hubault, 9 April, 1925).

(12) **SIMULIUM ANGUSTITARSIS** Lundström, 1912.

Larva.

Average length 6·9 mm. *Head* light brown with dark spots arranged as in *S. aureum*, but not enveloped in a cloud. Spots *a* and *d* always separate. An eye-brow with an enclosed dark spot present. Two chitinous apodemes in the posterior border ventrally, nearly meet in the middle line.

In all characters resembling *S. aureum*, except that in the latter the 2nd segment of the antenna is comparatively shorter. In the submentum, however, the anterior tooth of the pair on each side of the terminal row is not much enlarged.

Pupa.

Average size 4·0 × 1·4 mm. *Trichomes* longer than in *S. nölleri*; rows of cuticular spines present in segments 6, 7, and 8, and a few even in segments 5 and 9; *terminal spines* well developed; and the ventral spines as in *S. nölleri*.

Respiratory filaments (*G*, Text-fig. 17) 4·6 mm. long, 4 in number, arising more or less from the same point or may be arranged in shortly stalked pairs. The upper pair is distinctly swollen near the base, where the filaments are widely divergent, the uppermost nearly vertical.

Cocoon, average size 4·7 × 2·6 mm. as in *S. latipes*, except that the anterior process is much shorter (about 0·8 mm. long).

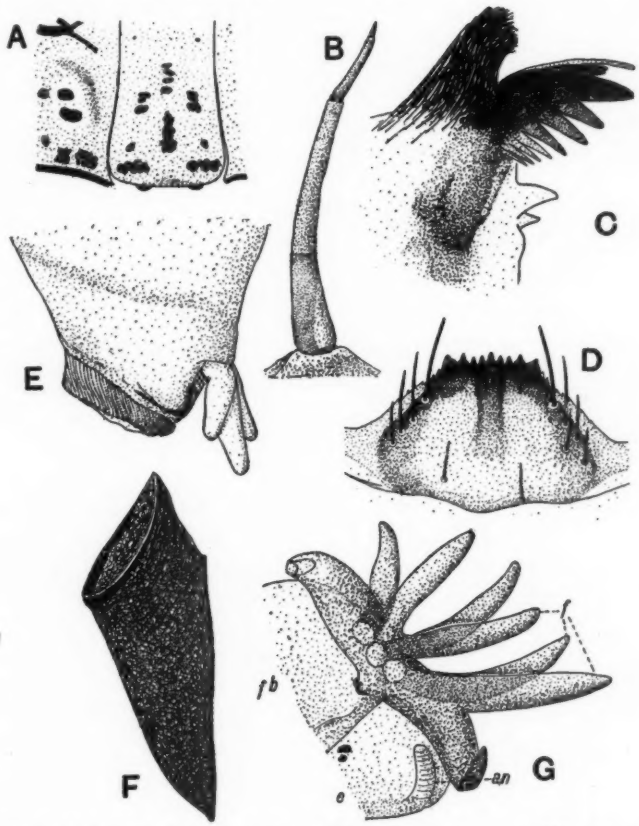
(13) **SIMULIUM EQUINUM** Linn. 1758, and Edwards 1915.

Larva.

Average length 7·0 mm. *Head* (*A*, Text-fig. 18) brownish-yellow with all groups of discs deeply pigmented and appearing as sharply defined dark spots without any enveloping dark cloud. Eye-brow absent or very faint with inconspicuous enclosed dark spot. *Antennae* (*B*) comparatively short, 4-segmented, 2nd segment about twice the length of the 1st and 3rd, which are about equal, sometimes 3rd segment a little shorter than the 1st. *Cephalic fan-filaments* number 46–53. *Mandibles* (*C*). 3 sub-equal teeth in row *s t*, in row *b t* only 4 or 5 teeth, and the processes *t p* as in *S. aureum*. *Submentum* (*D*) has 9 teeth in terminal row; 2nd tooth, from each side, much enlarged and

approaching the outer tooth in size. There are 4 or 5 hairs on each side below the submentum.

The *lateral cuticular plates* on each side of the thoracic proleg are comparatively larger than those in *S. nölleri* and the projections from its anterior margin are not arranged in groups.



Text-fig. 18. *S. equinum* L. LARVA. *A–E*, as in Text-fig. 7. PUPA. *F*, Side view of cocoon. *G*, Side view of the anterior end.
an, antenna; *e*, remains of larval eyes; *f*, pupal filaments; *f b*, base of the filaments.

Anal gills (*E*) simple. *Rectal scales* and ventral papillae absent. Rows in *posterior sucker* 97–105 with 17–29 hooks in each.

PUPA.

Average size 3·5 × 1·2 mm. *Trichomes* short; disc-like tubercles minute and very few in number. Rows of dorsal cuticular spines on the abdomen and terminal spines absent. Ventral hook-like spines very strong in segments 5,

6, and 7 but not in 4, which only occasionally shows a small strongly chitinised sensory hair.

Respiratory filaments (*G*) have the form of thin-walled lobe-like tubes, 8 in number, arranged as shown in *G*, Text-fig. 18. The outer surface of the filaments bears small spinous projections which appear as dark spots.

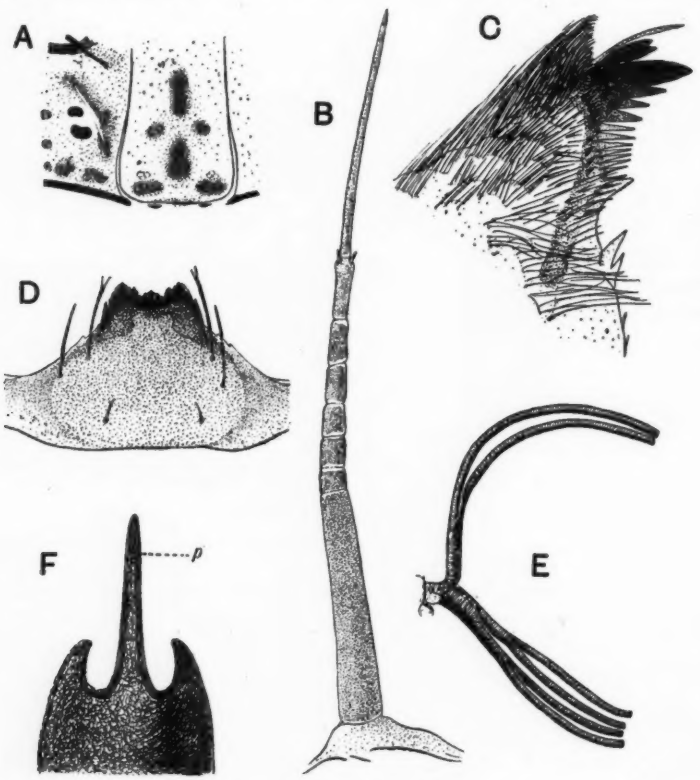
Cocoon (*F*), average size 4·8 × 1·7 mm., shoe-shaped, anterior margin nearly always thickened into a rim (incomplete ventrally). Floor absent in anterior half of cocoon.

Material collected. France: Many larvae found with *S. ornatum* Mg. from R. Mortagne, "Barrage de Mont" near Nancy (P. Remy, Jan. 1925).

(14) SIMULIUM SUBEXCISUM Edwards, 1915.

LARVA.

Length about 6·9 mm. *Head* (*A*, Text-fig. 19) pale yellow with all the groups of discs except *e* dark brown. On the frons-clypeus are six spots



Text-fig. 19. *S. subexcisum* Edw. LARVA. *A–D*, as in Text-fig. 7. PUPA. *E*, Respiratory filaments of right side. *F*, Anterior portion of cocoon from dorsal side. *p*, anterior process of the cocoon.

(*b* and *c* being confluent) of which *a* and *d* are the most conspicuous. A well-defined eye-brow present, with a sub-median black spot. Posterior end of eye-brow very dark. *Antennae* (*B*) very dark, long and slender. 9 segmented, 1st segment about as long as the next six together, and about six times as long as broad. The next six segments increase in length and decrease in thickness gradually from below upwards, 8th segment very slender and about equal to the 1st, and the 9th is minute. The two sensory projections are at the distal end of the 7th segment. *Cephalic fan-filaments* number 55–65. *Mandibles* (*C*) and other mouth-parts unlike the antennae, are very light in colour. Mandibles with 10–12 teeth in row *b t*, and 6–9 spinous projections behind them. Processes *t p* lie apart, the distal of the two nearly always bifid. *Submentum* (*D*) has 9 teeth in the front row and two on each side. Lamellar processes of the head capsule below the teeth are markedly serrated.

Anal gills simple. *Ventral papillae* as in *S. latipes*. *Rectal scales* absent. Rows in *posterior sucker* 75–85 with 10–12 hooks in each.

PUPA.

Average size 3·4 × 1·2 mm. *Trichomes* generally simple but occasionally one or two may be bifid. Cuticular tubercles very numerous and minute. Continuous rows of well-developed cuticular spines present dorsally on segments 5–9. Terminal pair of spines long. Pair of bifid ventral spines absent on segment 4.

Respiratory filaments, average length 3·1 mm., six in number arranged in pairs as shown in *E*, Text-fig. 19.

Cocoon (*F*), average size 4·0 × 2·2 mm., not closely woven, very much as in *S. latipes* except in the anterior process. In this species the dorsal wall of cocoon is produced forwards into a long process (about 2·0 mm.) with a thickened border, while in *S. latipes* only the thickened anterior border of the cocoon is produced into the process.

(15) SIMULIUM YERBURYI Edwards, 1920.

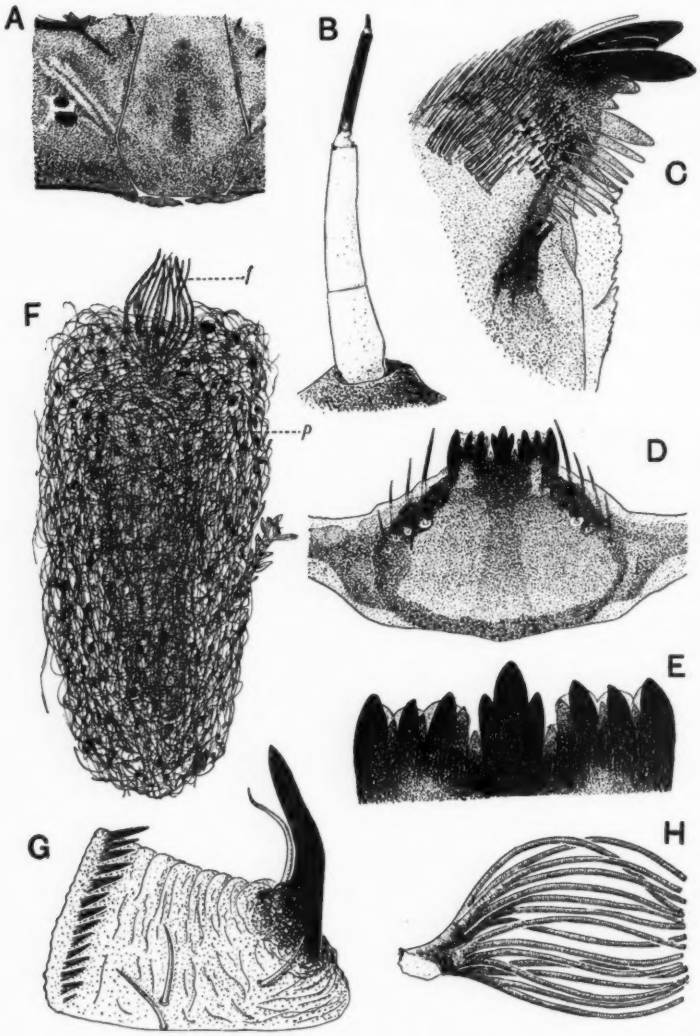
I have examined the pupal exuvia in the British Museum and have nothing to add to the following description already given by Edwards (1920): "Pupa—Differs from that of *S. subexcisum* as follows: Vertical stem of upper respiratory filaments shorter, forking near the base, each branch forking a second time at no great distance from the fork, so that there are eight branches in all."

(16) SIMULIUM HIRTIPES Fries, 1824.

LARVA.

Length 8·5–9·2 mm. *Head* (*A*, Text-fig. 20) dark brown, with groups of discs appearing as diffuse dark spots on frons-clypeus, which has a different shape from that in other species. Latero-posteriorly the head is very dark. Colourless area for the eyes small. Only an inconspicuous eye-brow present without a sub-median dark spot. *Antennae* (*B*) 4-segmented, chitinous wall of

two basal segments very thin and colourless, while that of distal segments is strong and dark. Two basal segments stout, 2nd about $1\frac{1}{2}$ times as long as



Text-fig. 20. *S. hirtipes* Fries. LARVA. *A–D*, as in Text-fig. 7. *E*, End of submentum. ×440. PUPA. *F*, Pupa *in situ* inside the cocoon. *G*, Lateral view of tergum of terminal segment. *H*, Respiratory filaments of right side.
f, filaments; *p*, pupa.

the 1st, 3rd very narrow and a little longer than 1st. Conical processes at the distal end of 2nd segment extremely minute and strongly chitinised. Rest of

the head-appendages very darkly pigmented. *Cephalic fan-filaments* number 35–45. *Mandibles* (*C*). First two of three teeth *s t* very small; 10 or 11 teeth in row *b t*. Instead of two teeth-like processes *t p* found in other species there is a single large process which extends along the distal half of the mandibles and has a serrated edge. *Maxilla* comparatively broader than in *S. nölleri* and has dorsally a thick cluster of long cuticular spines near the base of the palp, instead of 8–10 sensory hairs found on the maxillae of other species. *Submentum* (*D* and *E*) has 9 teeth in the terminal row but the lateral pair found in other species is absent. Three end-teeth of each side much enlarged and bifid, the outer division much stronger and darker than the inner. The central tooth is the largest in the row and is trifid. One tooth on each side of the central one is simple and very small. There are 4 or 5 long hairs on each side below the submentum. The pair of *lateral cuticular plates* on thoracic *proleg* are broad and strongly chitinised, and the number of processes, which are not arranged in groups, is large.

Anal gills simple and finger-like. Number of rows in *posterior sucker* about 90, with 10–13 hooks in each row. *Rectal scales* absent but a number of small pointed spines present on each side near the anterior limbs of the X-shaped sclerite. *Ventral papillae* absent.

Internal Anatomy. The four *mesenteric or gastric caeca* are extremely small, being very shallow, rounded protuberances. The last three ganglia of the *nerve cord* though lying close together, are separate from one another—not fused into one compound ganglion as in other species. There are ten pairs of well-marked closed *spiracles*, the tenth or last pair lying in the eighth abdominal segment. The tenth pair is much smaller than all the others and is situated dorsally on the larva. The initial thread connected to the tenth pair of spiracles arises in the eighth abdominal segment from the main tracheal trunk on each side.

Pupa.

Average length 4·7 mm. (longest 5·5 mm. and shortest 3·3 mm.) and breadth 1·5 mm. Pupa dark brown. The pair of *trichomes* on the head often bifid and there is a number of other sensory hairs in addition to those found in the other species. On each side of frons-clypeus along the line where the head-capsule splits when the image emerges, the cuticular tubercles are produced into short pointed hooklets. Thoracic trichomes long; they have the same number and arrangement as in other species. Cuticular tubercles not well-defined. Dorsally on the abdomen, hooks on segments 3 and 4 as in *S. nölleri*; complete rows of well-defined cuticular spines present along the anterior borders of segments 5–9; *terminal pair of spines* (*G*) strong and much enlarged with a sensory hair arising basally. Terminal segment bearing a number of long strongly chitinised sensory hairs. Ventrally a pair of strong cuticular hooks present on each side of segments 4–7 but sometimes only one, on segment 4; these hooks not bifid.

Respiratory filaments (*H*) about half as long as the pupa, 16 in number in pupae from Norway. The first division is near the base into three short stems, each of the two ventral stems dividing almost immediately into two branches, each of which bifurcates again. The upper stem again divides into three branches, the two lower ones dividing into three each and the upper into two. All the filaments are more or less of equal thickness and length.

In pupae from France, the arrangement of primary and secondary branches is exactly the same as that described above, but the tertiary branches subdivide irregularly a number of times so that the respiratory filaments attain a total number of 50–60.

As *S. hirtipes* Fries was originally described from Scandinavia, the pupae from Norway, with 16 respiratory filaments, must be regarded as typical.

Cocoon (*F*): average size 6·4 × 3·1 mm., consists of a light grey mass of loosely matted silk of no definite form, and more or less completely covers the pupa. Sometimes a number of cocoons together form one solid mass of matted silk, with pupae buried into it here and there.

Material collected: Larvae and pupae from mossy stones at the edge of a rapid river near Skagadalsben, Dist. Jotunheim, Norway (F. W. Edwards, Aug. 1923). *France*: Larvae and pupae from Clermont-Ferrand (E. Roubaud). Larvae with *S. monticola* Fried., from R. "La Vanage," near Servance, le Magny-Maubert (P. Remy, 9 Apr. 1925).

The larvae and pupae from Norway and France[1] resemble each other in every character, except in the number of respiratory filaments of the pupa. On dissecting out the male genitalia from advanced pupae I find, that they too are alike in the specimens from the two countries and resemble those of the British *S. hirtipes*. From this it seems very probable that the increase in the number of the respiratory filaments in the pupae from France, is merely due to a local variation, but as no adults (reared from pupae) are available nothing definite can be said.

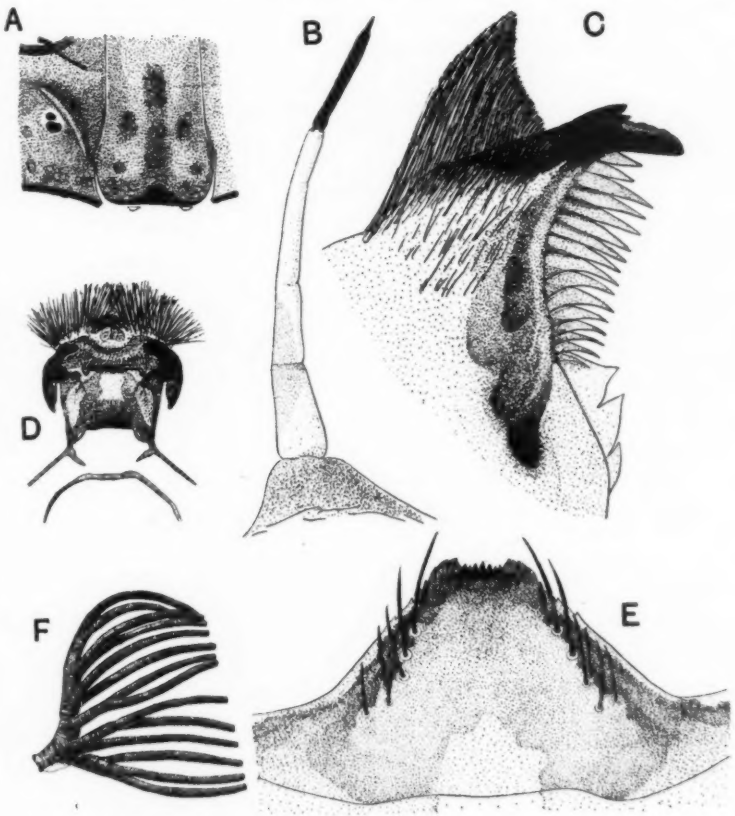
According to both Malloch and Johannsen, the pupae of *S. hirtipes* from America have a tuft of about 50–60 respiratory filaments on each side, but the arrangement of the branches—(primary, secondary and tertiary) as seen from their figures—is markedly different from that found in the pupae from Europe. As the arrangement of the branches is a very constant specific character, it seems probable that the species described from America may be an altogether different species belonging to the *hirtipes* group.

[1] I sent one of the male pupae from France to Mr F. W. Edwards for examination and in his letter to me dated 22 Nov. 1924 he writes: "I agree with you that there seems little or no difference in genitalia between this and British *hirtipes*, but I fancy the oedeagus is slightly different, also the first segment of the hind tarsi seems relatively a little longer in Roubaud's specimen, and the hind femur and tibia perhaps less hairy. One would like to see bred adults before giving an opinion as to whether these differences are specific or not. There are certainly several species of the *hirtipes* group, the females differing chiefly in the colour of the legs, which can't be seen in specimens dissected from the pupae (mature colouring being quite different from immature colouring very often). I should take the Norwegian *hirtipes* as typical, since the species was described from Scandinavia. Possibly the French specimens may be *rufipes* Mg. (= *fulvipes* Edw.) or *gallii* Edw. both only known from ♀."

(17) **SIMULIUM TREDECIMATUM** Edwards, 1920.

LARVA.

Average length 10·0 mm. *Head* (*A*, Text-fig. 21) dark brown with the groups of plates pigmented and appearing as diffuse dark spots. Spots *b c* darker than the others and the longitudinal patch *d* connected to a median dark area in the posterior border of frons-clypeus. A conspicuous eye-brow present with sub-median black spot. In some larvae, the head is very dark



Text-fig. 21. *S. tredecimatum* Edw. LARVA. *A–C*, as in Text-fig. 7. *D*, Dorsal view of hypopharynx and prementum. *E*, Ventral view of submentum. PUPA. *F*, Respiratory filaments of right side.

laterally and there is only a small white circle for the pair of eye-spots. Ventrally the thinly chitinised area extends about half-way under the submentum. *Antennae* (*B*) 4-segmented; 1st two segments membranous and more or less colourless and the distal two dark. 2nd segment about 2½ times as long as the 1st and 3rd, which are about equal, and 4th is minute. *Cephalic fan-filaments*

number 64–70. The bristles along the ventral edge of filaments are very thin and three or four times as long as in other species. *Mandibles* (*C*). The upper border of the large terminal tooth is thin and broadly serrated. Instead of the three teeth in row *s t* there are only two small ones as in *S. hirtipes*, while the 3rd has probably shifted into the row *b t* which has 14–16 teeth. Teeth-like processes (*t p*) are very broad and three in number. *Maxillae*, as in *S. hirtipes*. *Submentum* (*E*) has 11 teeth in terminal row (obviously one of the lateral teeth has grown forwards). The middle seven teeth are pointed and small, the central one being the longest of the seven, while the end teeth are very broad and form an almost continuous border. There are 4–6 long hairs on each side below the submentum.

Lateral plates on thoracic proleg as in *S. hirtipes* but less strongly chitinised.

Rectal scales and *ventral papillae* absent. *Anal gills* long and simple. Number of rows in *posterior sucker* 105–120, with 15–25 hooks per row.

Mesenteric or *Gastric Coeca* a little shorter than in *S. nölleri*.

Pupa.

Size 5·5 × 1·5 mm. *Trichomes* on head and thorax very short. Dorsally on the abdomen there is a row of 5 or 6 sensory hairs on each side, transformed into strong hooks in segment 2, and in segments 3 and 4 there are the usual rows of 8 strong cuticular hooks. Rows of cuticular spines are present only on segments 6, 7 and 8. Pair of terminal spines is absent. Ventral cuticular spines absent on segment 4. On nearly all segments, ventrally, there is a row of 8 to 12 sensory hairs transformed into strong hooks or spines which are bifid and peculiarly curled spirally in the posterior three segments.

Respiratory filaments[1] (*F*) very short as compared to the size of the pupa (being only about 1·5 mm. long). Their number varies from 11 to 14 on each side, sometimes differing even in the same individual. The first division is just near the base into four short stems, each of the two lower ones divides into two branches, one of which again bifurcates close to its origin. The third stem bifurcates near its base. The uppermost stem gives off from three to six branches which may arise in pairs or singly.

Cocoon, 6·5 × 2·3 mm., like that of *S. equinum* but becomes very thin in the region of the anterior border. The floor is absent in the anterior one-third of the cocoon.

Material collected. This species was described by Edwards from larvae found in a trout's stomach in England and nothing is so far known about their habitat in the British Isles or about the adult form. In August, 1923, Mr Edwards collected three larvae and one pupal exuvia (on which the above description of the pupa is based) together with larvae of *S. venustum* Say, *S. morsitans* Edw., and of other species from Tännforsen Falls, Sweden.

[1] Of the 17 larvae from which pupal respiratory filaments were dissected out, one had 11 on each side, three had 12 on one and 11 on the other, three had 12 on each side, four had 13, one had 14 on one and 13 on the other, while five had 14 on each side. The single pupa from Sweden had 14 filaments on each side.

SUMMARY OF PARTS I AND II.

(A) Life history.

(1) *Simulium* larvae are found in streams where the current is very fast. They are sedentary in habit and fix themselves to some support by means of their posterior sucker and sticky salivary secretion.

(2) Progression is achieved by looping movements which have been described in detail.

(3) Larvae feed on all kinds of fresh water animalcules, and algae.

(4) Two species were reared from eggs to the adult flies for the first time in the laboratory. Abundance of food and aeration of water are two very important factors governing the rearing of these larvae.

(5) There are six larval stages, each stage lasting 4–7 days. The gradual changes in the successive stages are described in *S. erythrocephalum* and *S. aureum*.

(6) The sixth-stage larva, having woven its cocoon, changes into a pupa, the whole process, weaving of cocoon and pupation (described in detail), takes 75–90 minutes. Pupal life lasts 5–15 days, depending on temperature.

(7) The eggs are sub-triangular in form and are laid in large patches on aquatic plants below the surface of water.

(8) The first-stage larva is characterised by the presence of an egg-burster situated dorsally upon the head.

(B) Morphology.

(9) The larvae are eucephalous, with eleven faintly marked body-segments, three thoracic and eight abdominal, the eighth abdominal being apparently divided into two parts, the posterior carrying the anus and posterior sucker. There is a median uniramous thoracic proleg which like the posterior sucker is provided with a number of cuticular hooks.

(10) The head has a number of markings which are of great taxonomic importance.

(11) The head-appendages are: A pair of jointed antennae, a rounded labrum, a pair of lateral fan-shaped appendages (the premandibular organs), a pair of mandibles, a pair of maxillae each with a single-jointed palp, a hypopharynx, and a labium. These appendages have been described in detail in this paper for the first time.

(12) The alimentary canal, malpighian tubules, salivary glands, muscular system and gonads are dealt with in detail.

(13) The oesophageal valve has no blood sinus as has been erroneously described by previous writers.

(14) A pair of dorsal glands are present above the pharynx. Their walls consist of large uninuclear cells. Dorsal glands have so far been found only in *Sciara* among Dipterous larvae.

(15) There is a well-developed central as well as visceral nervous system. The bilobed brain lies in the head and a chain of eleven ganglia in the body.

Both the supra-intestinal and the infra-intestinal visceral systems are fully worked out for the first time.

(16) There is a well-developed tracheal system with ten closed spiracles, one prothoracic, one metathoracic and eight abdominal.

(17) The flattened dorsal vessel stretches from the seventh abdominal segment to the head where it ends just behind the brain. It is dilated in the seventh segment to form the heart which is provided with two pairs of ostia.

(18) Nephrocytes or excretory cells (pericardial, and peri-oesophageal) are described for the first time and compared to similar structures in other Dipterous larvae.

(19) A detailed description of the early stages of all the known (seventeen)[1] British species is given, with remarks about eleven of them, as they occur in Sweden, Norway and France.

(20) The characters used for determining the species are as follows: *Larva.* Head markings; antennae; mandibles; submentum; anal gills; ventral papillae; and posterior sucker. *Pupa.* Chaetotaxy, Respiratory filaments, and Cocoon.

ACKNOWLEDGEMENTS.

To Mr F. W. Edwards of the British Museum, I am greatly obliged for his generous gift of material, and for the identification of the many specimens I have sent him. I have also to thank Dr M. Langeron (Paris), Dr E. Roubaud (Paris), Mr E. Séguy (Paris), Prof. L. Léger (Grenoble), Mr P. Remy (Nancy), Mr E. Hubault (Nancy) and Mr A. W. Rymer Roberts (Cambridge) for supplying me with material and the last-named also for his assistance in revising part of the manuscript for the press. To Prof. G. H. F. Nuttall, Director of the Molteno Institute, I owe sincere gratitude for the keen interest he has taken in my work. I am highly indebted to Dr D. Keilin, also of this Institute, for his unfailing kindness and the very ready and constant manner in which he has put at my disposal his great knowledge of Dipterous larvae.

Finally, my warmest thanks are due to Sir Dorabji Tata for his generous financial aid without which this work could not have been carried out to completion.

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[1] Note while going through the press: Mr Edwards has added an eighteenth species, the early stages of which are not yet known.

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(*MS. received for publication* 16. VI. 1925.—Ed.)

ON THREE NEW PROTEOCEPHALIDS (CESTODA) AND A REVISION OF THE GENERA OF THE FAMILY.

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(With 18 Text-figures.)

When La Rue (1914 *a*) published his exhaustive monograph on the Proteocephalidae, all the then-known species of this family were, with one exception, shown to be very much alike. To substantiate this statement it will suffice to mention that all the six genera, into which La Rue grouped the species, were chiefly based upon trivial characters of the scolex and the distribution of the testes. The one exception referred to was the species which he re-named *Monticellia coryphicephala* (Monticelli), and this species differed from all the others in the remarkable and relatively deep-seated character of its principal genital organs being situated in the cortical region of the parenchyma instead of in the medullary. This one exception was promptly transferred by La Rue to a distinct new family, the Monticellidae, and the consequence was that he was still left dependent upon the aforesaid trivial characters as bases for his genera in the original family. Since 1914 however we have come to know of some other Proteocephalids exhibiting similar deep-seated differences of structure, and we are therefore in a position to re-consider the classification of the Proteocephalidae on broader lines, including *Monticellia coryphicephala* in that family. The general scheme of this re-classification I have already outlined in a paper (Woodland, 1925 *a*) which will be published either before or shortly after the present communication, and it is my purpose, in this latter, to justify the suggestions there referred to by discussing the subject in some detail. Before attempting this, however, I shall describe the structure of three new Proteocephalids, two from India (in a frog and a Varanid lizard) and one from the Sudan (in a Siluroid fish).

PART I. NEW PROTEOCEPHALIDAE.

Proteocephalus tigrinus, n.sp.

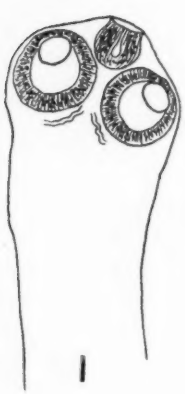
This Cestode was found in the duodenum or anterior intestine of the common Indian frog, *Rana tigrina*, at Allahabad, United Provinces, India. Only three specimens were obtained in three frogs out of at least two hundred frogs examined at Allahabad, Lucknow and Agra; the species is therefore a rare one. The species is also of interest, not only as regards several of its

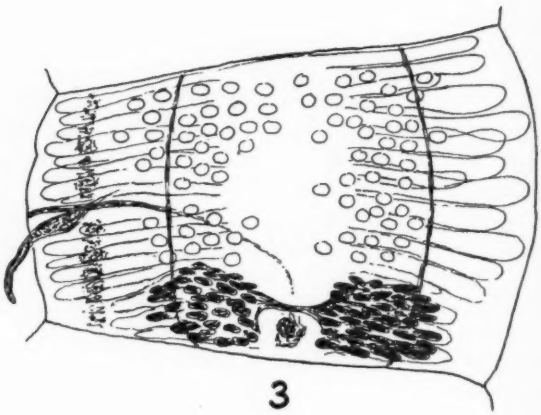
structural traits but because it is only the third species of Proteocephalid to be described from the Anurous Amphibia ("*Ophiotaenia*" *schultzei* (Hungerbühler), 1910, from *Rana adspersa*, and "*Ophiotaenia*" *hylae* Johnston, 1912, from *Hyla aurea*, from South Africa and Australia respectively, being the other two) and the sixth from Amphibia in general (see La Rue, 1914 *a*, p. 284, who describes "*O.*" *filaroides* La Rue from *Amblystoma tigrinum* and "*O.*" *lönnbergii* (Fuhrmann) from *Necturus maculosus*, but omits reference to "*O.*" *schultzei*, and, 1914 *b*, for "*O.*" *cryptobranchi*).

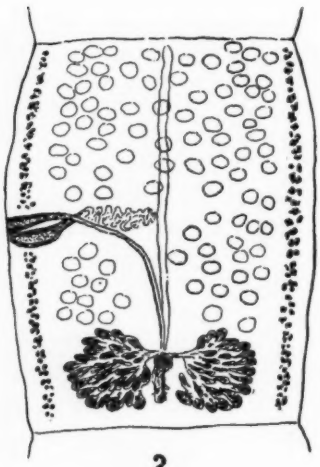
Proteocephalus tigrinus is a small white worm. I am unable to give the total length of any one of my three specimens because they were not measured when found and they have since been cut into pieces and either flattened between glass slides or sectionised, and all I can state, with any certainty, is that all three specimens were about 30–40 mm. in total length, with a maximum breadth of about 1·39 mm. They were therefore smaller than either "*O.*" *schultzei* (45–90 mm.), "*O.*" *hylae* (more than 60 mm.), "*O.*" *filaroides* (80–110 mm.), "*O.*" *lönnbergii* (170–190 mm.) or "*O.*" *cryptobranchi* (300 mm.).

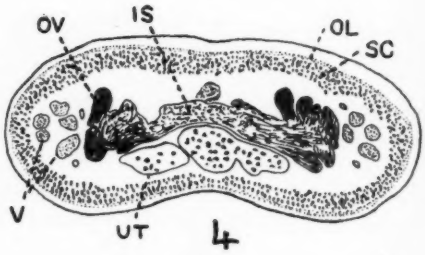
I possessed two scolices (unflattened) but owing to one becoming lost during re-staining, the following description is based on the remaining one (though I had previously examined the lost specimen), which I first drew as a whole and later sectionised. The scolex is small (0·233 mm. broad and 0·146 mm. long from apex to base of suckers) and is not delimited from the neck (Fig. 1). The four suckers face upwards and outwards, are about 0·091 mm. in diameter, have circular openings and, with all other parts of the scolex, are devoid of spinelets. The apex of the scolex is slightly prominent and bears a spherical organ, with very thick walls, small slit-like lumen and an opening at the extremity. I cannot speak as to its nature but it is apparently neither a functional apical sucker nor a mere "muscle plug" remnant of a muscular rostellum. It probably resembles the similar structure found in "*O.*" *hylae* (absent in the other Amphibian "*Ophiotaenia*"). The unsegmented neck is about 1·49 mm. long and 0·149 mm. broad. A fairly long neck also characterises each of the other five Amphibian Proteocephalids.

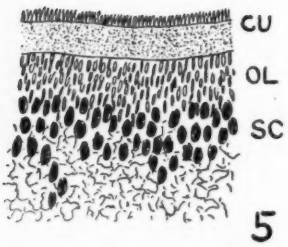
Mature proglottids vary in shape according to their position in the strobila and their state of contraction. In my artificially flattened (in the case of the more elongated proglottids only very slightly) and therefore distorted preparations some are distinctly broader than long $\left(\frac{\text{1·42 mm. broad}}{\text{0·71 mm. long}}\right)$, others longer than broad $\left(\frac{\text{0·86 mm. broad}}{\text{1·29 mm. long}}\right)$, and the same statement applies to ripe proglottids, some unflattened ripe proglottids measuring $\frac{\text{1·39 mm. broad}}{\text{1·16 mm. long}}$ and $\frac{\text{0·99 mm. broad}}{\text{1·21 mm. long}}$, and some much-flattened ripe proglottids measuring $\frac{\text{2·18 mm. broad}}{\text{1·77 mm. long}}$ and $\frac{\text{1·06 mm. broad}}{\text{2·06 mm. long}}$. The sides of the proglottids are more

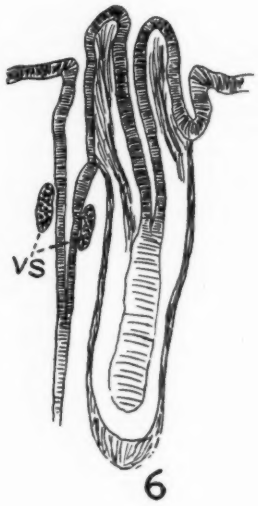












Figs. 1–6.

(when broader than long) or less (when longer than broad) salient, though the corners do not project nor the hind borders overlap succeeding proglottids. The genital apertures are irregularly alternate and open midway in the length of the proglottid.

The ovary, viewed from the surface, is, as usual, bi-lobed and each lobe is approximately circular in outline and is composed of a number of large follicles (Fig. 2). The vagina, oviduct and shell-gland all lie dorsal to the isthmus connecting the two lobes of the ovary, the ventral side of the ovary being occupied by the hind part of the uterus, which extends, in ripe proglottids, to the extreme posterior border of each proglottid. The testes are numerous (about 70–110 in number) and are situated anterior to the ovary and dorsal to the uterus, in a single field (Fig. 2), so differing from the two-lateral-field condition found in the other known Amphibian Proteocephalids, though La Rue admits that in "*O.*" *lönnbergii* the "midzone of the proglottid is not entirely free of testes." They measure (in transverse sections—all my toto-preparations having been flattened) about 0·033 × 0·024 mm. The cirrus sac opening is usually posterior to the vaginal aperture but occasionally the reverse is the case. The cirrus sac measures about 0·201 mm. in length by 0·051 mm. in maximum breadth and extends roughly over about one-fifth of the breadth of the proglottid. It contains no coils of the ductus, its walls are distinctly muscular and it is apparently protrusible (Fig. 6). The cirrus is unarmed. The vas deferens is very much convoluted outside the cirrus sac, the thick mass of coils extending to the middle line of the proglottid. The vagina opening is situated close to and on a horizontal level with the base of the cirrus and is often placed on an eminence. A sphincter vaginae is present. The vagina is dilated in the vicinity of the cirrus sac but in no other part, so far as I could ascertain, and, when anterior to the cirrus sac, passes inwards ventrally to the sac. The vitellaria are of the usual type and measure about 14 × 11 microns. The uterus is also of the usual type and when fully developed consists of a very wide central passage (artificially widened in flattened sections of course, Fig. 3), from which arise some 15–20 diverticula on each side, these extending as far out as the vitellaria. The central passage and

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LEGENDS TO TEXT-FIGURES 1–6.

Figs. 1–6. *Proteocephalus tigrinus.*

CU, cuticle; *IS*, isthmus of ovary; *OL*, outer (subcuticular) layer of longitudinal muscles; *OV* ovary; *SC*, nuclear layer of subcuticula; *UT*, uterus; *V*, vitellaria; *VS*, vaginal sphincter.

Fig. 1. Scolex. (×116.)

Fig. 2. Mature proglottid, slightly flattened. Ventral view. (×52.)

Fig. 3. Ripe proglottid, much flattened. Dorsal view. Note great width of the median chamber of the uterus, in part due to flattening. The eggs are not shown. (×36.)

Fig. 4. Transverse section across a young ripe proglottid in the region of the ovary. Note the absence of an internal longitudinal muscle sheath and the presence of the egg-filled uterus ventral to the ovary. (×74.)

Fig. 5. The body-wall seen in transverse section. (×213.)

Fig. 6. The vaginal aperture and the partly-protruded cirrus seen in a horizontal section. (×240.)

diverticula extend ventral to the ovary (a noteworthy feature, possibly correlated with the absence of an internal longitudinal muscle sheath) back to the hind border of the proglottid and are only separated from the uterus in the next proglottid behind by a thin septum. The eggs, which are not well preserved in my preparations, are freely scattered in the uterus and the embryos measure (in sections) about 11 microns in diameter.

One important distinctive feature of *P. tigrinus* is the total absence in mature proglottids (and immature, so far as I can ascertain) of the inner longitudinal muscle layer, the cortical region of the parenchyma thus being indistinguishable from the medullary (Fig. 4). Beddard (1913 *a*) has noted the same feature in several species of "*Ichthyotaenia*" from *Varanus niloticus*. La Rue remarks that in "*Ophiotaenia*" *filaroides*, "*O.*" *lönnbergii* and "*O.*" *cryptobranchi* this layer of muscles is "weakly developed," though apparently not absent. Apart from a few dorso-ventral fibres, the parenchyma of *P. tigrinus* contains no muscles whatever, though there is a distinct outer layer of longitudinal muscles in the subcuticula (Fig. 5). Two excretory vessels are present on each side, the ventral one having much thicker walls than the dorsal vessel.

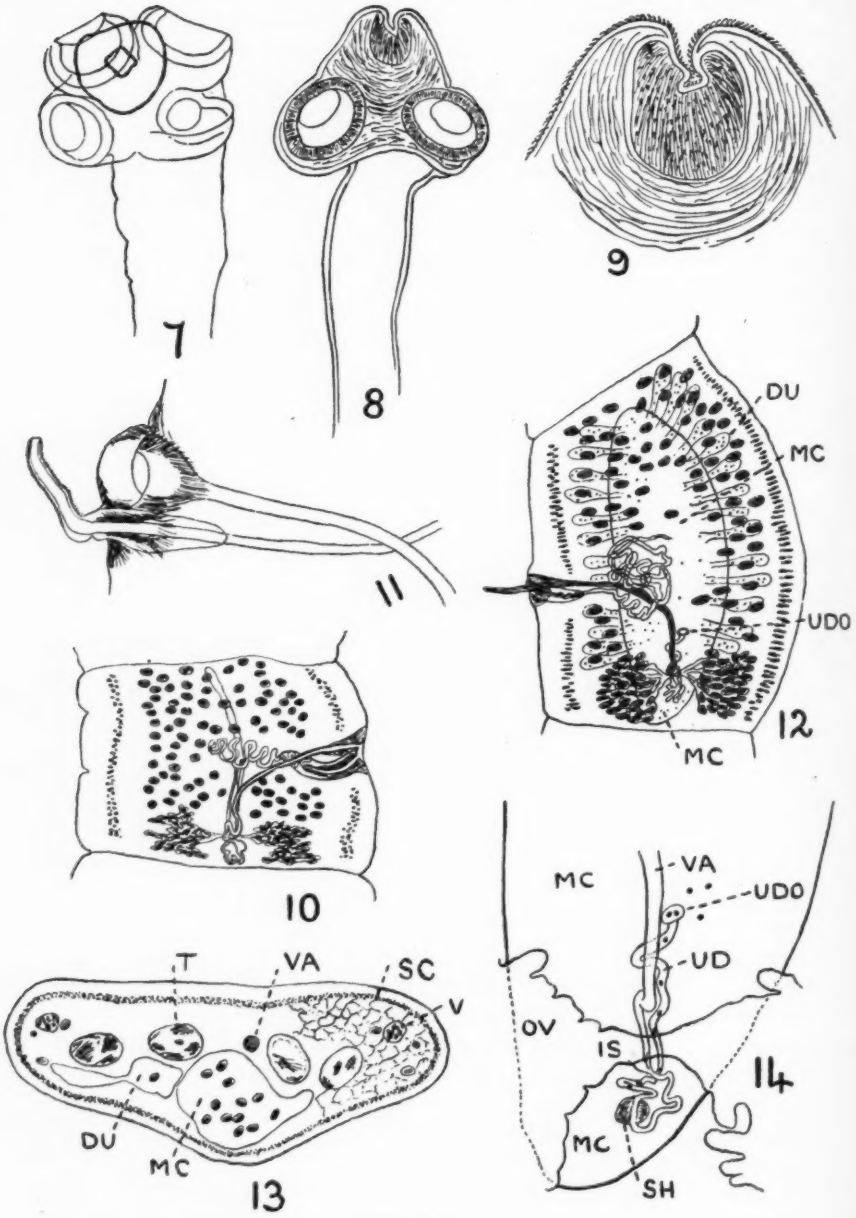
Proteocephalus beddardi, n.sp.

Of this species I possess more than thirty specimens procured from the anterior and middle regions (isolated proglottids were also found on one occasion in the hind region) of the intestine of *Varanus bengalensis*, a fairly large monitor very common in the United Provinces, as in other parts of India. Many of my best specimens have been more or less broken up into separate pieces and flattened between glass slides when alive and fixed in that condition, but, judging from other formalin-preserved unflattened nearly-entire specimens, I should say that the worms range in length from about 40–80 mm. Their maximum breadth, when in formalin and unflattened, is about 0·8 mm.

I possess only four mounted scolices, the covering of cuticular spinelets undoubtedly having caused most of the scolices to remain attached to the intestinal mucosa when the worms were removed. The scolex is pyramidal in shape (Figs. 7, 8), consisting of a prominent apex ("rostellum") and a four-lobed base, each lobe carrying a sucker, and is sharply delimited from the neck. The lobes are capable of considerable protrusion, the suckers in one of my scolices projecting greatly. An apical organ was present (Fig. 8), globular in form and closely resembling a typical muscular rostellum and apparently devoid of a lumen, though its front end was invaded by a well-marked depression of the terminal cuticle (lined with conspicuous cuticular spinelets, Fig. 9). It appears to be an organ also capable of protrusion and partial eversion and may be boring in function. The scolex (in balsam) is about 0·259 mm. broad at its base and about 0·212 mm. long. The suckers are about 0·102–0·109 mm. broad and face upwards and outwards. The whole of the

scolex is covered with closely-set cuticular spinelets, which extend backwards over the neck and for a short distance over the anterior indistinctly-segmented strobila. The unsegmented neck is about 0·5 mm. long and about 0·099 mm. broad, *i.e.* about half the breadth of the base of the scolex.

The strobila, despite its weak musculature, appears to be capable of considerable local extension, the shape of mature segments varying, in my material, from a nearly square form up to an elongated strip, nine times longer than broad. The segmentation is very evident in stained transparent specimens, and is also visible in opaque specimens owing to the slightly salient sides of the segments (more conspicuous in the short segments), though the proglottids in no way overlap each other and do not possess projecting corners. Mature segments, as just stated, vary greatly in form—a variation not solely due to their having been flattened. In my flattened material, young mature proglottids may vary from $\frac{0{\cdot}530 \text{ mm. broad}}{0{\cdot}249 \text{ mm. long}}$ (*i.e.* broader than long; *vide* Fig. 10) up to $\frac{0{\cdot}295 \text{ mm. broad}}{2{\cdot}773 \text{ mm. long}}$ (*i.e.* nine times longer than broad). An average flattened mature segment measures about $\frac{0{\cdot}215 \text{ mm. broad}}{0{\cdot}249 \text{ mm. long}}$. Fully-ripe proglottids (only found in one worm) show (Fig. 12) in my limited material, no such extreme variations of shape, since they only vary from about $\frac{0{\cdot}448 \text{ mm. broad}}{0{\cdot}415 \text{ mm. long}}$ to about $\frac{0{\cdot}365 \text{ mm. broad}}{0{\cdot}830 \text{ mm. long}}$, and the average ripe proglottid is about square (0·464 mm.). The genital apertures are, as usual, irregularly alternate, and they open at about the middle of the proglottid length; the cirrus and vaginal apertures irregularly alternate as to which is anterior. In non-extended flattened proglottids the cirrus sac reaches across about a quarter of the breadth of the proglottid, but in extended proglottids, with a proportionately-narrowed breadth, it may reach half-way across. The actual length of the cirrus sac in my toto-preparations naturally varies according to the degree of flattening and state of extension of the proglottid, but in transverse sections of unflattened material, it is about 0·128 mm. in length and about 0·051 mm. in depth. In the cirrus sac with the cirrus non-extruded, the cirrus with its ejector muscles occupies the major and outer part of the sac, the small inner end being occupied by a few coils of the ductus; when, on the other hand, the cirrus is everted and extruded (Fig. 11), the ductus in the sac becomes more or less straight and the sac itself much shortened. The cirrus is well armed with cuticular spinelets—a feature also described by Beddard (1913 *a*) as being present in "*Ichthyotaenia*" *nilotica*, but apparently absent in all other "*Acanthotaenia*" species though present in "*Ophiotaenia*" *punica* (Southwell and Adler, 1923) and "*Crepidobothrium*" *amphiboluri* (Nybelin, 1917). The wall of the cirrus sac is fairly thin and I doubt if it is muscular. The cirrus and the vagina both open into a very shallow atrium, the latter opening just below



Figs. 7–14.

the former. The vagina is enlarged at its opening (this region being of about the same size as the cirrus sac), becomes narrow behind the cirrus sac, often shows a slight dilatation (in non-extended proglottids) midway in its course between its opening and the ovary, and its narrow portion just anterior to the ovary usually (in non-extended proglottids) shows several coils. The vagina lies on the ventral side of the vas deferens. The convolutions of the vas deferens form a more or less compact mass lying in the middle line of the proglottid (Fig. 12). The testes are about 60–80 in number and measure in transverse sections of unflattened proglottids about 55 × 30 microns as a maximum. In distribution the testes exhibit on the whole neither a strictly *Proteocephalus* (*i.e.* uniformly distributed in one field) nor a strictly "*Ophiotaenia*" (*i.e.* distinctly segregated into two lateral fields) condition but rather in-between conditions varying between the two extremes. In some non-extended proglottids the testes are almost typically *Proteocephalus* in distribution, in others (a few) almost typically "*Ophiotaenia*," the remainder showing intermediate conditions, though the testes are usually more numerous peripherally than centrally. In the elongated extended proglottids the testes, as might be expected, tend more towards a uniform one-field distribution. Since transverse sections of unflattened proglottids show that the testes are almost always to be found in or near the middle line, I propose for this and other reasons to be supplied later to label the species *Proteocephalus*. The vitellaria are normal in distribution and measure individually about 25·6 × 14·6 microns. The ovary is, as usual, bi-lobed and each lobe is obviously made up of elongated follicles, which, in extended segments, are widely separate from each other. The surface-view area of the ovary of course varies with the state of extension of the proglottid but the area is considerable even in short proglottids.

Concerning the ducts in the neighbourhood of the ovary, it is to be noted that both the vagina and the posterior portion of the primitive uterine strand run dorsal to the ovarian isthmus, assuming that the dilated uterus with its contained eggs lies next to the ventral side of the proglottid. Later, in ripe

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LEGENDS TO TEXT-FIGURES 7—14.

Figs. 7–14. *Proteocephalus beddardi.*

DU, diverticula of uterus; *IS*, isthmus of ovary; *MC*, median chamber of uterus; *OV*, ovary; *SC*, nuclear layer of subcuticula; *SH*, shell gland; *T*, testes; *UD*, uterine canal; *UDO*, opening of uterine canal into median chamber of uterus sac; *V*, vitellaria; *VA*, vagina.

Fig. 7. Scolex in outline. (× 116.)

Fig. 8. Another view of the scolex showing the apical organ (muscular rostellum?). (× 116.)

Fig. 9. The apical organ seen in optical section, with the spinelets. (× 346.)

Fig. 10. A young mature proglottid. Dorsal view. (× 52.)

Fig. 11. The cirrus sac, armed cirrus and vaginal opening from the ventral aspect. The vaginal opening is somewhat distorted. (× 74.)

Fig. 12. Ripe proglottid, much flattened, in dorsal view. Note the wide median chamber of the uterus sac and the presence of the uterus below the ovary. (× 23.)

Fig. 13. Transverse section (anterior to the uterine canal) across a young ripe proglottid. Note absence of the internal longitudinal muscle sheath. (× 116.)

Fig. 14. The ducts in the region of the ovarian isthmus, viewed from the dorsal side. (× 74.)

segments, the primitive uterine strand becomes separated into two very distinct parts—a *uterine canal*, which represents the hind fifth of the primitive uterine strand, and which runs dorsal to the ovarian isthmus, and the *egg-storing uterus*, or *uterus proper*, which consists of a ventrally-placed wide median sac—the *median chamber of the uterus*—which extends backwards below the ovary (as in *P. tigrinus*) to near the hind limit of the proglottid, and *lateral diverticula* which arise laterally from the median chamber on both sides and throughout the whole length of the proglottid. In ripe proglottids the dorsal narrow uterine canal can be seen to run anteriorly to the ovary and to open by a small definite aperture into the wide ventral median chamber, with its diverticula (Fig. 14). I could detect no definite egg-ejector (schluckapparat), but a large shell-gland is present, a short distance behind the ovarian isthmus. The ovary lies nearer the dorsal surface than the ventral. I could detect no uterine pores and I am fairly certain that they are not pre-formed. In this connection it may be mentioned that proglottids become cast off from the strobila long before they are fully ripe; in fact, well before the uterus has developed so far as to contain eggs. I am unable to state definitely the exact number of uterine diverticula owing to these being obscured in my preparations by the large testes but I would suggest that there are about fifteen to twenty on each side, possibly more. The eggs contained in the uterus measure about 19·3 × 14·6 microns.

In transverse sections of developed proglottids (Fig. 13) the longitudinal musculature is seen to consist solely of a slender band of fibres lying immediately outside the nuclear layer of the subcuticula; in other words, the wide-meshed parenchyma is, as in *P. tigrinus*, not subdivided up into medulla and cortex by the presence of an internal layer of longitudinal muscles. The longitudinal musculature thus being feebly developed, it is perhaps surprising that the proglottids should exhibit such different conditions of extension, but I suspect that, the contractile musculature being so weak, those individual proglottids which were in an extended condition when the host was examined were unable to contract themselves previous to being fixed by the reagents employed.

Southwell (1916, p. 15) obtained "numerous specimens" of what was undoubtedly this species from the same host—*Varanus bengalensis*—in Orissa, near the Chilka Lake, and he identified them with the "*Ichthyotaenia*" *nilotica* described by Beddard (1913 *a*), from *Varanus niloticus* (specimens deposited in the London Zoological Gardens). Now quite apart from Beddard's remark (based on very limited data) that "our knowledge of these parasites of *Varanus* shows so far that, while a particular species of *Varanus* may harbour more than one species of *Ichthyotaenia*, the same species of *Ichthyotaenia* does not infest more than one species of *Varanus*," it seems improbable that *V. bengalensis* captured in India should contain the same Proteocephalid species as *V. niloticus* captured in Africa, and a comparison of the species I have described above with that described by Beddard tends to confirm this contention,

though the two species are undoubtedly very much alike. The principal differences are (*a*) that *P. beddardi* is distinctly larger than "*I.*" *nilotica* (the latter species only being about 30 mm. long and 0·5 mm. broad); (*b*) that in the former species there is no "lack of a definite break between the reproductive systems of each segment," *i.e.* there is no "appearance of complete continuity" such as Beddard describes; (*c*) that the genital apertures in my species usually open exactly midway in the length of the proglottid but occasionally slightly behind this point and never "slightly in front," as is normally the case in "*I.*" *nilotica*; (*d*) that the ovary of *P. beddardi* is not "solid" like that of "*I.*" *nilotica*; and (*e*) that the eggs in the uterus are never "aggregated into masses"; and (*f*) possess a very distinct shell. Beddard omits to mention in his description a number of details which would aid differentiation of these two species, such as *e.g.* the number of the testes and the dimensions of these and other organs and the differentiation or not of the definitive uterus into the narrow uterine canal and the spacious uterine chamber and pouches. Coupled with the *à priori* improbability of the two species being identical, the few differences I have enumerated above justify me, I think, in assuming that the species I have described is new, and I name it in honour of an authority who has contributed largely to our knowledge of Cestodes.

For convenience of reference I will here append a list of the principal of those Proteocephalid species which have been or can be relegated to the very doubtful genus *Acanthotaenia* v. Linstow in virture of the scolex and anterior strobila being covered with minute cuticular spinelets.

"*Ichthyotaenia*" *biroi* v. Ratz, 1900, from *V.* sp., New Guinea.
„ *saccifera* v. Ratz, 1900, from *V.* sp., New Guinea.
"*Acanthotaenia*" *shipleyi* v. Linstow, 1903, from *V. salvator*, Ceylon.
„ *tidswelli* Johnston, 1910, from *V. varius*, *V. gouldii* and *V. bellii*, Australia.
"*Ichthyotaenia*" *nilotica* Beddard, 1913, from *V. niloticus*, Africa.
„ *varia* Beddard, 1913, from *V. varius*, Australia.
„ *gracilis* Beddard, 1913, from *V. varius*, Australia.
"*Acanthotaenia* (*Ophiotaenia*)" *striata* Johnston, 1914, from *Lialis burtonii* (a limbless lizard belonging to the Pygopodidae), Queensland.
"*Acanthotaenia*" *varia* Nybelin, 1917, from *V. gouldii* Gray, South Queensland (from Nybelin's description this worm is probably specifically distinct from Beddard's "*I.*" *varia* and should be re-named).
Proteocephalus beddardi Woodland, 1925, from *V. bengalensis*, India.

I shall discuss the validity of the genus "*Acanthotaenia*" later.

PROTEOCEPHALUS SYNODONTIS, n.sp.

This interesting species was obtained from the intestine of the Nile Siluroid *Synodontis schall* Bloch-Schneider, in the neighbourhood of Khartoum, by the late Dr A. J. Chalmers, when Director of the Wellcome Tropical Research Laboratories at Khartoum. The chief feature of interest is the almost total obliteration of the cortical region of the parenchyma by the extraordinary development of the internal layer of longitudinal muscles—a condition which is the exact antithesis of that found in *P. tigrinus* and some Varanid "*Acan-*

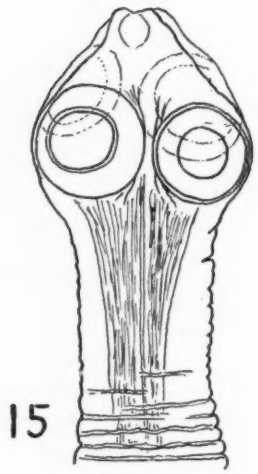
thotaenia," and which, in its excessive development, makes the species, so far as I am aware, unique among Proteocephalidae. My material, unfortunately, is very limited. I possess a scolex and about 9 mm. of attached immature proglottids and four separate portions (5–10 mm. in length) of strobila consisting entirely of ripe proglottids, all stained and mounted in balsam. I possess no mature proglottids, *i.e.* with undeveloped uterine diverticula. I also have a fair number of horizontal and transverse sections but these also are all of ripe proglottids and do not form perfect series. I am naturally unable to give the total length of any one specimen of this worm but, judging from the fragments I possess, I should say that the complete mature worms are at least 30 mm. in length and probably much longer. The maximum breadth of my fragments is 1·5 mm.

The scolex (Fig. 15) is pyramidal in shape, consisting of a fairly prominent "rostellum," *i.e.* prolongation of the apex of the scolex, which is marked by four longitudinal grooves, and a quadrilobular base, each swollen lobe of which is mainly occupied by a large sucker and is separated from adjacent lobes by the continuation of the grooves on the apex. The scolex has a maximum breadth of 0·614 mm. and is 0·547 mm. long, from the apex to the base of the suckers. The suckers measure about 0·298 mm. in diameter and have circular openings facing sideways, and, as already remarked, they are borne on the four, probably protrusible, lobes. An apical organ is apparently present on the top of the rostellum but my single specimen is not sufficiently good to allow me to make out its structure. Spinelets are entirely absent. Below the suckers powerful longitudinal muscles are to be seen passing down from the scolex into the neck for a distance of at least half a millimetre. I cannot state the length of the unsegmented neck because, owing to the numerous secondary transverse grooves (lined by the exceedingly thick cuticle) which commence at a distance of half a millimetre behind the suckers, all traces of true proglottidisation are obscured, and lack of material prohibits me from cutting sections. The breadth of the anterior 0·5 mm. of neck is 0·373 mm. and is therefore less than that of the scolex.

The neck and strobila are encased in a very thick cuticle—thicker than that on the scolex—and, as just mentioned, very numerous secondary transverse grooves are present over the whole of the strobila (Fig. 16), save for the most anterior half millimetre of neck. These cuticular grooves, combined with the extraordinarily thick internal layer of longitudinal muscles, effectually obscure most of the details of structure which, in most worms, can be seen easily in toto-preparations. In some elongated proglottids the vitellaria, testes and ovary can be seen vaguely (Fig. 16) but that is all of the internal anatomy. On the other hand, the true limits of the ripe proglottids can be determined by the slight lateral constrictions which are present between proglottids and by the position of the genital openings. Ripe proglottids vary in shape between $\frac{1{\cdot}294 \text{ mm. broad}}{0{\cdot}581 \text{ mm. long}}$ and $\frac{0{\cdot}472 \text{ mm. broad}}{2{\cdot}950 \text{ mm. long}}$, according to their position in the

strobila and state of contraction. The genital apertures are irregularly alternate and are situated a little in front of the middle transverse line of the segment. The cirrus and vaginal apertures also irregularly alternate as to which is anterior. The cirrus sac is cut across in one of my transverse sections and is there 0·215 mm. long and 0·099 mm. in maximum breadth (dorso-ventrally, at the innermost end), and is at most one-seventh of the breadth of the proglottid (in very elongated proglottids the sac extends across one-third of the breadth). It contains coils of the ductus in its innermost half. The cirrus, when fully everted, apparently does not involve eversion of the sac, is unarmed, swollen at the base, and is equal in length to about half the breadth of the proglottid. The coils of the vas deferens, in fully-ripe proglottids, are mostly massed at the base of the cirrus sac, being pushed aside by the enormous uterus. The vagina opens dorsal to the cirrus opening (Fig. 18), is slightly dilated in the region of the cirrus sac but apparently not elsewhere, and it is somewhat convoluted in front of the ovary in non-elongated segments. The ovary, in surface view, is broad, both laterally (extending to the vitelline strands) and antero-posteriorly, and in transverse section is at least a quarter of the thickness of the proglottid (Fig. 17). The middle piece joining the two lobes can hardly be called an isthmus, since it is about half as broad antero-posteriorly as the "lobes" and like them consists of ovarian follicles (Fig. 17) and not merely of transverse ducts. The vagina and the uterine canal both pass dorsal to the median piece of the ovary. The uterus, as seen in ripe proglottids, consists of the dorsal uterine canal and the ventral median sac and lateral diverticula. The egg-storing portion of the uterus does not extend ventral to the ovary. The diverticula number about twenty on each side (so far as I can estimate), are quite narrow when seen in horizontal sections (in which they extend right up to the vitellaria), but very deep when seen in transverse sections. The median uterine sac has about four downgrowths in each proglottid, which open as usual on the ventral surface (Fig. 16). I was unable to make out any details of the ducts behind the ovary but I think there is a shell-gland. The vitellaria form as usual two thin lateral strands. The testes in ripe proglottids are of necessity arranged in two distinct lateral fields, owing to the medianly-developed large uterus, but whether two lateral fields are present before the uterus becomes swollen with eggs I am unable to say, but I think it is probable (cf. *Proteocephalus malopteruri*; see Woodland, 1925 *a*). The testes in horizontal sections of ripe proglottids measure about 95 × 51 microns. The eggs possess two shells, the diameter of the outer thicker shell being about 18 microns and of the embryo 11 microns.

The most remarkable feature of this species is the almost entire obliteration of the cortical region of the parenchyma by the enormous development of the inner longitudinal muscle sheath (Figs. 17, 18). The cortex is entirely occupied by the muscle fibres save for a narrow area on the ventral median surface, and even this area is not present throughout the entire length of the proglottid. This condition, as already remarked, is the exact antithesis of the condition



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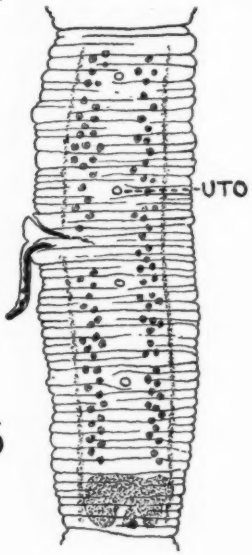

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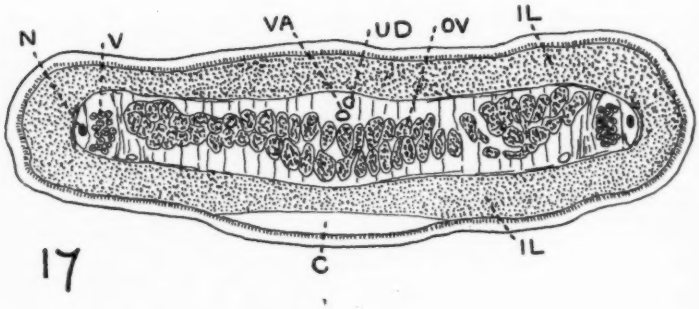

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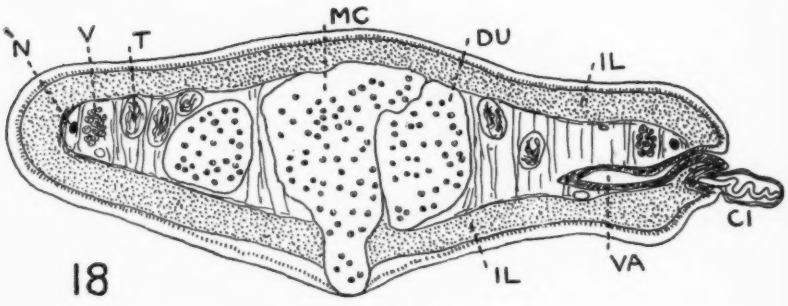

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Figs. 15–18.

seen in *P. tigrinus* and *P. beddardi*, and some other species described by other authors (*e.g.* Beddard in "*Ichthyotaenia*" *nilotica*, 1913 *a*), in which the cortex is also absent as such, since, owing to the entire lack of an internal longitudinal muscle sheath, it is continuous with and indistinguishable from the medulla. In addition to this very thick internal layer of longitudinal muscles and the usual thin sheath of outer longitudinal muscles, situated immediately external to the nuclear layer of the subcuticula, a number of conspicuous dorso-ventral muscle fibres are present and also transverse fibres lying immediately on the inner side of the internal longitudinal muscle sheath. The parenchyma is very wide-meshed with thin inconspicuous fibres. Beddard (1913 *b*) has described the cortex of "*Ichthyotaenia*" *marenzelleri* as being, in the region of the neck, wholly occupied by a "very thick layer of longitudinal muscle fibres," but the individual fibres were "rather far apart," and, compared with the layer I have described, extremely sparse, and certainly did not obliterate the cortical parenchyma.

PART II. ON THE GENERA OF THE PROTEOCEPHALIDAE.

Some thirteen more or less recognised genera[1] have altogether been proposed in which to allocate the numerous species of Proteocephalid Cestoda, viz. *Proteocephalus* Weinland, 1858 (syn. *Ichthyotaenia* Lönnberg, 1894: *vide* La Rue, 1914 *a*); *Marsypocephalus* Wedl, 1861; *Corallobothrium* Fritsch, 1886; *Crepidobothrium* Monticelli, 1899; *Acanthotaenia* von Linstow, 1903; *Choanoscolex* La Rue, 1911; *Ophiotaenia* La Rue, 1911; *Monticellia* La Rue, 1911; *Ophidotaenia* Beddard, 1913; *Solenotaenia* Beddard, 1913; *Rudolphiella* Fuhrmann, 1916; *Goezeella* Fuhrmann, 1916; and *Gangesia* Woodland, 1924. Of these thirteen genera two can at once be eliminated without much discussion. *Ophiotaenia* has been shown by Nybelin (1917) to be synonymous

[1] When writing my previous paper (1924 *b*) I was unaware of Fuhrmann's important communication (1916) describing *Rudolphiella* and "*Goezeella*"; hence my lack of reference to these genera in the aforesaid paper. I may add that it was purely by chance that I happened to discover Fuhrmann's paper when describing a genus somewhat similar to *Rudolphiella* (Woodland, 1925 *a*), since the *Zoological Record* for 1916 contains no mention whatever of the important morphological facts stated by Fuhrmann (as it should have done under the heading of "Structure"), nor cross-references to the new genera he described under the name of "*Corallobothrium*."

LEGENDS TO TEXT-FIGURES 15—18.

Figs. 15–18. *Proteocephalus synodontis.*

C, cortex; *CI*, cirrus; *DU*, diverticula of uterus; *IL*, internal layer (sheath) of longitudina muscles; *MC*, median chamber of uterus; *N*, nerve; *OV*, ovary; *T*, testes; *UD*, uterine canal; *UTO*, opening of uterus to exterior; *V*, vitellaria; *VA*, vagina.

Fig. 15. Scolex in outline. (×52.)

Fig. 16. Semi-transparent view of an elongated ripe proglottid. (×36.)

Fig. 17. Transverse section across a ripe proglottid in the region of the ovary. Note in this and the next figure the enormous development of the internal longitudinal muscle sheath, which obliterates the cortex save for a small area in the median ventral line. (×74.)

Fig. 18. Transverse section across a ripe proglottid in the region of the cirrus sac. (×74.)

with *Crepidobothrium*. The genus *Crepidobothrium* was founded solely upon the very indefinite and trivial external character of re-entrant (*i.e.* notched) posterior margins of the suckers, but though this character, as Lühe (1899) remarked, is altogether too insignificant upon which to found a genus, yet the name *Crepidobothrium* remains, on grounds of priority, and replaces "*Ophiotaenia*," the name given by La Rue to species possessing testes arranged in two lateral fields, since Monticelli's "*Crepidobothrium*" possesses this latter feature. *Ophiotaenia* is thus disposed of and with it Beddard's *Ophidotaenia*, which is a synonym[1].

Of the remaining eleven genera, three, viz. *Monticellia*, *Rudolphiella* and *Marsypocephalus*, are so well founded upon indisputable well-marked characters of the internal structure that we may accept them without hesitation (Fuhrmann, 1916; Woodland, 1925 *a*). On the other hand, the generic classification of the species remaining (the vast majority) after we have separated the five species which appertain to the three genera just named, is a matter of considerable difficulty, not only on account of the apparent or real absence of prominent distinguishing features and lack of definite detailed information concerning certain features of the internal anatomy which might possibly serve for the required purpose, but chiefly because of the different classificatory values attached by different authorities to certain characters. Of the eight remaining genera five are based upon characters of the scolex (either in combination with or apart from other characters) and the remaining three, viz. *Proteocephalus*, *Crepidobothrium* and *Solenotaenia*, are based respectively on the residue of characters which remain after other genera have been constituted, on the two-field distribution of the testes, and on a peculiarity of the uterus (Beddard, 1913 *c*)[2]. Now it is evident that for a single character to be regarded as valid for the founding of a genus, this character should, as far as possible, be of a deep-seated nature affecting the internal organisation. Such deep-seated characters are those of the uterus utilised by Lühe in his

[1] In my previous paper (1924 *b*, footnote on p. 448) I erroneously stated that, with Beddard's "*Ophidotaenia*," Shipley's genus "*Palaia*" (Shipley, 1900) and Sonsino's "*Panceria*" ("*Pancerina*," *vide* Sonsino, 1895, and Stossich, 1895) must be regarded as synonyms of *Proteocephalus*. The former may be, though the attachment of the worm to the intestine by the burrowing into it of the entire scolex and the unilateral arrangement of the genital apertures render this rather doubtful. As regards the latter, this, like the former, is too imperfectly known to be placed with certainty in any scheme of classification but apparently the presence of a double set of reproductive organs definitely excludes it from the genus *Proteocephalus*. The founding of genera on imperfect material is greatly to be deprecated.

[2] In the original unabbreviated MS. of this paper I had included a full re-description of Beddard's "*Solenotaenia*" *viperis* and had given my reasons for not regarding this species as worthy of serving as the type of a distinct genus. These reasons, in brief, are that although the uterus of this species differs from that of all other known species in the development of the peculiar and conspicuous ventral groove, yet this groove after all represents, physiologically if not morphologically, only a fusion of uterine pores, and the stunted diverticula, associated with the groove in "*Solenotaenia*," are also to be found in several other Ophidian Proteocephalids, as *e.g.* *P. marenzelleri*, *P. calmettei* and "*Crepidobothrium*" *gerrardii*. "*Solenotaenia*" *viperis* therefore only differs from certain other Proteocephalid species in a relatively trivial external character.

classification of the sub-family Ptychobothriinae, the duplication of the genitalia (as in *Amphitretus* and *Dipylidium*), the cortical or medullary situation of organs (as seen in genera of the Bothriocephalidae and in *Marsypocephalus*, *Rudolphiella* and *Monticellia*), well-marked differences of proportionate lengths and positions of internal organs (as in *Wenyonia* and *Caryophyllaeus* e.g.) and differences in number and position of internal organs (as in many genera of Cyclophyllidea). The alternative to single deep-seated characters is a constant combination of characters of less importance which are easily recognisable. I also assume that a multiplicity of genera is in itself not desirable, since it leads to the artificial separation of forms which, if grouped in one genus, are recognised as being closely allied.

The five genera founded upon scolex characters are *Corallobothrium*, *Choanoscolex*, *Acanthotaenia*, *Goezeella* and *Gangesia*. Now *Corallobothrium* and *Goezeella*, with *Rudolphiella*, are all three characterised by the well-known corolla-like formation of skin lappets on the scolex, and if this scolex character is to be recognised by itself as of generic value, these three genera should all be grouped in one genus, *Corallobothrium*, but, as Fuhrmann (1916) has shown, these differ fundamentally as regards the cortical and medullary situation of the genital organs and therefore the corolla character must take a subsidiary place, *i.e.* as one of at most sub-generic value. It is evident from this one fact that the corolla character (one of the most conspicuous of the scolex characters found in Proteocephalidae) must have originated independently in three very distinct species and if this be the case, it is further evident that this, and other less conspicuous scolex characters, cannot serve as stable deep-seated characters for taxonomic purposes. The only alternative to this conclusion is to assume that the corolla character is the stable one and (1) that the different situations of the genital organs relative to the internal longitudinal muscle sheath, seen in "*Corallobothrium*," "*Goezeella*" and *Rudolphiella*, have arisen in the "*Corallobothrium*" genus; and (2) that the arrangement of the genital organs seen in *Monticellia* has arisen independently in a distinct genus. But this I, for one, cannot credit, because not only is the arrangement of the genital organs of *Monticellia* practically identical with that of "*Goezeella*," but the two species agree in such details as the shape of the ovary and the lateral extent of the vitellaria. I assume therefore that the corolla type of scolex has originated independently in the three genera named. Fuhrmann retains the corolla character as one of generic value, but only in combination with the other characters. Thus he maintains *Corallobothrium* (otherwise identical with *Proteocephalus*) and creates *Goezeella* (otherwise identical with *Monticellia*) solely on account of their possession of the corolla. Taking into consideration however the exceedingly low value, if any, of such scolex characters as generic characters (Woodland, 1923, 1924 *a*, *b*, 1925 *a*) I propose that the presence of mere lappets of skin on the scolex, like re-entrant notches on the suckers, shall be considered as only of specific value and that the genera *Corallobothrium* and *Goezeella* shall lapse. I am confirmed in this opinion by the lack of value,

as generic characters, of other and more solid features of the scolex. In the Proteocephalidae there is apparently a complete evolutionary series of apical organs, ranging from minute indeterminate bodies (such as exists in Beddard's "*Solenotaenia*" *viperis*) up to a well-defined apical sucker (as is stated to occur in certain species of *Proteocephalus* from Teleosts), on the one hand, and, on the other hand, *via* such apical organs as those to be seen in Nybelin's "*Acanthotaenia*" *varia* (1917) and my *P. beddardi* (described above), to well-developed typical muscular rostella, as seen in my "*Gangesia*" (1924 *b*) and in Fritsch's "*Taenia*" *malopteruri* (see Woodland, 1925 *a*). If we attempt to group together forms with similar apical organs, we soon discover that these afford no guide whatever as to true affinities. For example, we should be compelled to group together forms like "*Gangesia*" and Fritsch's "*Taenia*" *malopteruri*, which differ from each other in other far more essential characters (form of uterine diverticula and distribution of testes *e.g.*). Again in Bothriocephalidae I have shown (1925 *a*) that the genus *Clestobothrium* contains a species (*C. clarias*) possessing a type of scolex which Lühe employs as a principal diagnostic character for his genus *Ptychobothrium*. From these facts (and from others better known, such as *e.g.* the structure of the scolices of *Taenia solium* and *T. saginata*) I conclude that the scolex characters mentioned (and *à fortiori* still more trivial characters such as the presence of hooks and spinelets) certainly cannot serve as characters of generic value by themselves, and I therefore propose the abolition, as genera, not only of *Corallobothrium* and *Goezeella*, but also of *Choanoscolex* and my own genus *Gangesia*, since all these genera are solely or chiefly based on scolex characters.

As to whether these or other scolex characters can serve for the definition of genera from the point of view of being constantly associated with certain other characters, the evidence seems to incline against this course also. We have seen that the corolla character is associated with very different types of distribution of the internal organs (in "*Corallobothrium*," *Rudolphiella* and "*Goezeella*") and the genera "*Choanoscolex*" and *Gangesia* possess only one and two species respectively. In connection with the genus *Acanthotaenia*, on the other hand, it is stated by Nybelin (1917) that in the Proteocephalids infesting the lizard family Varanidae the spiny investment of the scolex is always correlated with certain other scolex characters, viz. small size, cone-shaped rostellum carrying an apical sucker, hemispherical suckers, and with certain proglottid characters, viz. a thin-walled vagina, lacking or with only a weakly-developed sphincter vaginae, small thin-walled cirrus sac, weak-muscled cirrus, loose distribution of testes, and weak general musculature, and he claims that this association of numerous, individually insignificant, features justifies the retention of the genus. Similarly Johnston (1910) re-defined the genus *Acanthotaenia* by associating with the spiny scolex the non-scolex characters of ill-marked external segmentation of the strobila, single genitalia, lateral irregularly-alternating genital openings, numerous testes usually in two fields, bi-lobed posterior ovary, shell-gland behind ovary,

lateral vitellaria, vagina opening in front of or behind cirrus, uterus median and tubular and carrying diverticula, thin-shelled eggs and genital ducts passing between the longitudinal excretory vessels.

But these non-scolex characters adduced by these two authors are to be found, singly and probably to a large extent collectively (*e.g.* most of Nybelin's characters in *Proteocephalus exiguus*), in many other Proteocephalids altogether devoid of spiny scolices, and even if they were, collectively, diagnostic of Varanid Proteocephalids, they are too inconspicuous and indefinite for practical use. Moreover, they are outweighed by the more obvious differences which obtain between the several "*Acanthotaenia*" species. *E.g.* in "*A.*" *shipleyi* and in "*A.*" *nilotica* and "*A.*" *varia* the testes are said to be situated in one field, whereas in "*A.*" *tidswelli* and some other species, the testes are situated in two fields; again in "*A.*" *shipleyi* and "*A.*" *biroi* the cirrus is stated to be constantly posterior to the vagina, whereas in "*A.*" *gracilis*, "*A.*" *saccifera* and "*A.*" *tidswelli* the reverse is usually the case, and in "*A.*" *varia* always the case; finally in "*A.*" *nilotica*, "*A.*" *varia* and *P. beddardi* there is no trace of an internal longitudinal muscle sheath, and probably in all three the egg-filled uterus extends ventral to the ovary, whereas in "*A.*" *tidswelli* a conspicuous muscle sheath is present and, judging from Johnston's description of the ovary being situated near the ventral surface, the uterus does not extend beneath it. Further it is now known that a number of other species, which certainly do not possess collectively the non-scolex characters listed by Nybelin, show spinelets on the scolex—the character supposed to be distinctive of "*Acanthotaenia*": such as the *Proteocephalus gallardi* of Johnston (from the Australian black snake, *Pseudechis porphyriacus*), *P. malopteruri* (Fritsch's "*Taenia*" *malopteruri*; *vide* Woodland, 1925 *a*), *P. osculatus* (from a Siluroid fish in Germany) and the two species of "*Gangesia*" recently described by me (1924 *b*) from Indian Siluroids. This character of scolex spinelets is therefore not constantly correlated with certain other characters and therefore cannot serve in this connection to define a genus. If its retention as a generic character be insisted upon, several genera will have to be created according to the different sets of other characters with which it is associated.

From the preceding I think it will appear that we cannot utilise scolex characters for the definitions of genera, either by themselves or in conjunction with other characters, since in very many cases species which are most unlike as regards their strobila possess similar scolices and, *vice versa*, many forms, similar to each other in proglottid anatomy, possess widely-different scolices.

A non-scolex character most relied upon, after scolex characters, by La Rue, is the one- or two-field distribution of the testes, but in this case also we are faced with the same difficulty, viz. that it cannot be employed by itself as a diagnostic feature, and that, if we employ it in conjunction with other characters, we shall be compelled to create a separate genus for every different set of characters with which it is associated. The one-field and two-field distributions of the testes are, to a very large extent, found indiscriminately

scattered among the Proteocephalids belonging to very different hosts. For example, the Proteocephalids of fresh-water Teleosts nearly all have their testes arranged in one field[1], whereas in all those found in Ophidia the testes are arranged in two fields, but, on the other hand, in "Ganoid[2]" and Siluroid[2] fishes, Amphibia[3], Varanidae[4] and Chelonia[5], the Proteocephalids show either both conditions or intermediate conditions. We are compelled to conclude then that testes distribution can only occasionally be employed as a character which will aid in defining a group, and certainly does not serve for the diagnosis of a distinct genus.

Since, in my opinion, neither scolex characters, nor characters such as testes distribution, relative positions of the cirrus and vaginal apertures, or number, position and form of uterine diverticula, approach in value the character upon which the three genera *Monticellia*, *Rudolphiella* and *Marsypocephalus* are founded, the only logical course is to regard, at least for the present, all Proteocephalid species, other than the five included in these three genera, as species in one large genus *Proteocephalus*. I therefore proceed to diagnose these four genera, previous to a brief consideration as to whether or not it is possible provisionally to subdivide the genus *Proteocephalus* into a number of groups or sub-genera.

The genus *Monticellia* La Rue may be defined as follows: Proteocephalidae with the "testes, vitellaria and uterus entirely outside of the inner longitudinal muscle sheath. Vitellaria composed of scattered follicles which form broad lateral fields," mostly ventral in position. Testes lie in a single broad dorsal field between vitellaria. "Uterus ventral, with many lateral pouches." Ovary situated dorsally largely outside the longitudinal muscle sheath. Found in Siluridae from Europe and S. America.

This genus comprises two species: Monticelli's "*Tetracotylus*" *coryphicephala* (= *M. coryphicephala*) and Fuhrmann's "*Goezeella*" *siluri* (= *M. siluri*).

The genus *Rudolphiella* Fuhrmann may be defined as follows: Proteocephalidae with the testes and vitellaria in the cortex, *i.e.* outside of the inner longitudinal muscle sheath. Vitellaria form broad lateral fields, ventro-lateral in position. Testes lie in a single broad dorsal field between vitellaria. Uterus in the medulla and ventral in position, with many lateral pouches. Ovary situated dorsally, with small projections from the lobes penetrating the upper part of the internal longitudinal muscle sheath. Found in Siluridae from S. America.

This genus was first described by Riggenbach (1896) under the name of *Corallobothrium lobosum*, and contains only one species—*Rudolphiella lobosa* (Riggenbach).

[1] *P. longicollis* Zeder (from Salmonidae) appears to be an exception.

[2] *Vide infra.*

[3] See my account of *P. tigrinus* for examples.

[4] Examples given above in connection with "*Acanthotaenia.*"

[5] In "*Tetrabothrium*" *trionychinum* Lönnberg the testes are in one field, while in "*Ophiotaenia*" *testudo* Magath the testes are in two fields.

The genus *Marsypocephalus* Wedl may be defined as follows: Proteocephalidae with the testes situated in the dorsal cortex in a single field; all other organs medullary. Vitellaria and all other organs as in *Proteocephalus*. In Siluridae, from Egypt and the Sudan.

This genus was first[1] fully described by the present writer (1925 *a*) and contains two species: *M. rectangulus* Wedl and *M. heterobranchus* Woodland.

The foregoing three genera are thus based upon the situation of the genital organs relative to the internal longitudinal muscle sheath. But it is necessary to call to mind that in certain other species the distinction between medulla and cortex is altogether lost owing to the total absence of the muscle sheath. Beddard, *e.g.* (1913 *a*), has described the absence of this muscle sheath in several species from *Varanus niloticus* and *V. varius* and the same peculiarity is described above for *P. tigrinus* and *P. beddardi*, but this character is apparently not associated with any other character (save perhaps the ventral extension of the egg-filled uterus under the ovary) or characters (the muscle sheath is present in the "*Acanthotaenia*" *tidswelli* described by Johnston from *Varanus varius*, e.g.) and there appear to exist transitions between a well-developed internal longitudinal muscle sheath and its total absence (in the Ophidian *Proteocephalus viperis* described above, *e.g.*, the muscle sheath is very feebly developed), so that even though, in many of these cases in which the cortex and medulla are indistinguishable, some of the genital organs clearly intrude into the cortical area, yet this intrusion is not comparable with that described for the three genera defined. Another peculiar condition is that above described in the case of *P. synodontis*, where the cortex becomes obliterated (save for a minute area on the ventral surface) owing to the excessive development of the internal longitudinal muscle sheath, but here

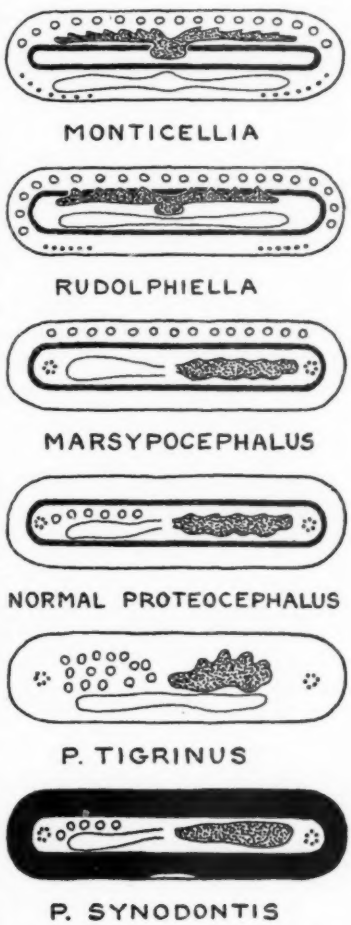

Fig. 19. Diagrams to illustrate the principal modes of disposition of the genital organs relative to the internal longitudinal muscle sheath in Proteocephalidae.

[1] Fuhrmann has prior claim. See Postscript, p. 394.

again such a feature cannot be used for taxonomic purposes, since there may exist all transitions between this and the normal Proteocephalid condition.

The fourth genus *Proteocephalus*, now intended to include all the remaining species of Proteocephalidae, may be defined as follows: Proteocephalidae with all the reproductive organs situated either in the medullary region of the parenchyma (where this is distinguishable from the cortex) or in the undivided parenchyma (when the internal longitudinal muscle sheath is absent). Vitellaria lateral, follicular, the follicles being closely grouped about a central conducting tubule. In fresh-water fishes, Amphibia and Reptilia.

Is it possible to subdivide into easily recognisable distinct groups all the numerous species contained in this large genus *Proteocephalus*? This is a question which it is almost impossible to answer at present for the simple reason that so many lacunae exist in our knowledge of the details of proglottid anatomy of these forms, but it may be worth while to attempt the definition of two groups which have been recognised. The Proteocephalids of fresh-water Teleostean fishes certainly appear to form one homogeneous group or sub-genus, which may be termed *Teleostotaenia* (the name *Ichthyotaenia* being of course inadmissible). This group is characterised by a usually small scolex (maximum breadth rarely more than 0·5 mm.[1] and usually less) with little or no projection of the apex beyond the suckers (rostellum) and total absence of hooks and spinelets, with the testes distributed in one continuous field[2], and with the vagina opening always situated anterior to the cirrus opening. This group contains all the Proteocephalids from fishes listed by La Rue (1914 *a*), save some from "Ganoids" and Siluroids.

A second large group, which may provisionally be labelled *Crepidobothrium*, is that in which the scolex is large or small, with a small rostellum or without one, with or without an apical organ and usually devoid of spinelets[3], with the testes usually to some extent or entirely segregated into two lateral fields, and with vaginal and cirrus apertures irregularly alternating as to which is anterior. This group is typically found in Ophidia[4] but owing to the vagueness of the definition it will also include many Proteocephalids found in Amphibia, Siluroids and Chelonia, while others, evidently closely allied to the forms included, will be excluded. In Amphibia, *e.g.* Fuhrmann's "*Ichthyotaenia*" *lönnbergii* conforms to the definition (although the testes are not completely

[1] In Faust's recently-described (1920) *P. ptychocheilus* from *Ptychocheilus oregonensis* Rich., the scolex is 1 mm. broad and the entire worm 200 mm. long.

[2] As before remarked, *P. longicollis* Zeder (from Salmonidae) is stated by von Linstow to have the testes in two fields.

[3] Johnston's *P. gallardi* has spinelets on the scolex.

[4] This group includes the forms recently described by MacCallum (1921) under the names of "*Tetrabothrius*" *boae* (30 *feet* long!), "*T.*" *lachesidis* (75 mm. long) and "*T.*" *brevis* (15 inches long). The reason why this author labels these obvious Proteocephalids "*Tetrabothrius*" is not apparent, nor why he repeatedly states, in the year 1921, that "the vagina curves towards the center to join the uterus" (!!!), and regards the shell gland as a vitelline gland. The other and very remarkable Cestodes described by this author are evidently Onchobothriidae, though labelled "*Taenia*."

separated into two fields) but La Rue's "*Ophiotaenia*" *filaroides* has the vagina opening always anterior to the cirrus sac. Johnston's "*Ophiotaenia*" *hylae* has the testes in two fields but again the vagina is anterior to the cirrus, while in Hungerbühler's "*I.*" *schultzei*, with testes in two fields, the vagina is behind the cirrus. In my *P. tigrinus*, on the other hand, the testes are in one field (the vagina usually being anterior to the cirrus). In "Ganoid" fishes, the two species *P. sulcatus* and *P. pentastoma* both have the testes disposed to some extent into two fields but in both the vagina is posterior to the cirrus sac. In Siluroid fishes some Proteocephalids have the testes in two fields and alternating vagina and cirrus apertures (*P. malopteruri* and *P. synodontis*, e.g.) but others have the testes in one field and with either alternating vagina and cirrus (as in *P. solidum*, syn. "*Corallobothrium*," and "*Gangesia*" spp.) or with the vagina anterior to the cirrus (*P. fossatus*) or posterior to the cirrus (as in *P. sulcatus*, which is also found in a Siluroid—*Clarotes*). In Chelonia I have already pointed out that while "*O.*" *testudo* has the testes in two fields, "*Tetrabothrium*" *trionychinum* has the testes in one field (in both species the vagina is anterior to the cirrus). It is thus fairly evident that the characters of testes distribution and the position of the vagina relative to the cirrus are of very little use.

As regards the sub-genus "*Acanthotaenia*" I have already disposed of this, so far as this is possible from the data to hand, but I might remark that the *P. tigrinus* described above bears a strong resemblance to certain species of "*Acanthotaenia*" as regards the absence of the internal longitudinal muscle sheath and the extension of the egg-filled uterus ventral to the ovary. Whether these similarities (so far only described in *P. tigrinus*, *P. beddardi* and the two or three species of "*Ichthyotaenia*" described by Beddard) constitute proof of affinity I do not know, but they are of more weight than many characters utilised by systematists in this group.

It is evident from the foregoing that it is almost impossible at present to substantiate distinct sub-genera in the genus *Proteocephalus*. Probably some deep-seated differences of structure will be discovered in the future which will serve the purpose[1] but until these have been ascertained it is advisable to avoid the subject and for the present to label all species *Proteocephalus* which evidently do not belong to the other three genera. Lühe came to a similar conclusion in 1899 when he wrote: "Die einseitige Rücksichtnahme auf den Scolex ist bei den sog. 'Tetrabothriden,' zu welchen ja auch die Ichthyotaenien gehören, besonders verlockend und hat hier auch schon Unheil genug gestiftet. Ich bin gern bereit zuzugeben, dass dereinst vielleicht auch die Ichthyotaenien wieder eine Auftheilung erfahren müssen, aber vorläufig

[1] For example it would be interesting to know whether "*Teleostotaenia*" is always characterised by the vagina and uterine canal passing ventral to the ovarian isthmus. In *P. beddardi*, *P. naiae*, *P. viperis*, *P. marenzelleri* and *P. synodontis*, and in *Marsypocephalus* spp. and *P. malopteruri* (forms not belonging collectively to any one of the sub-groups at present recognised) these two ducts always pass dorsal to the isthmus. According to Johnston (1912) it would appear that in "*Ophiotaenia*" *hylae* the vagina passes dorsal and the uterine canal ventral to the ovary!

ist unsere Kenntnis der überwiegenden Mehrzahl der hierher gehörigen Arten noch viel zu gering, um eine solche Auftheilung zuzulassen."

Finally I may remark upon the extraordinary variety of form among Proteocephalids found in Siluroid fishes. In two species from Indian Siluroids, which I named *Gangesia wallago*[1] and *G. macrones*, the scolex bears a large muscular rostellum armed with a circle of typical hooks and the suckers bear spinelets, and in Fritsch's "*Taenia*" *malopteruri*, from a Siluroid in the Sudan, the scolex also bears a muscular rostellum, which is armed with a broad band of very minute but true hooklets and the entire scolex and neck is covered with "*Acanthotaenia*" spinelets, but, apart from these similarities, these Indian and Sudanese Siluroid Proteocephalids certainly show nothing more in common with each other than with other fish Proteocephalids or with *Acanthotaenia*" species; in fact less, since in "*Gangesia*" the testes are evenly distributed in one field, while in the Sudanese form the testes lie in two distinct lateral fields. Again, *Proteocephalus osculatus* from *Silurus glanis* in Germany has a small apical "Saugnapf" which "mit zahlreichen, sehr hinfälligen Häkchen von 0·007 mm. länge besetzt ist" (Lühe, 1910), and, on this basis, La Rue seriously asks himself whether this species should not be placed in "*Acanthotaenia*" (despite the facts that this species is from a fish and that the testes are in one field) but decides that, since it is found in a Siluroid, it may possibly belong to *Monticellia* (!), but this of course was previous to our recently-extended knowledge of Siluroid Proteocephalids. We also find in Siluroids the three remarkable genera *Monticellia*, *Rudolphiella* and *Marsypocephalus*, the "*Ichthyotaenia*" *abscisa* ("*Choanoscolex*") of Riggenbach (with a fold of tissue at the base of the scolex partially enveloping the oval suckers), the "*Corallobothrium*" *solidum* of Fritsch (within its scolex corolla), and the *Proteocephalus synodontis* described in the present paper (with the internal longitudinal muscle sheath obliterating the cortex). Further, as Beauchamp (1918) suggests, it is probable that Diesing's "*Ephedrocephalus microcephalus*" and "*Zygobothrium megacephalum*," both from the Brazilian Siluroid *Phractocephalus hemiliopterus*—worms with scolices more extraordinary than that of "*Corallobothrium*"—are also to be regarded as Proteocephalids.

From the foregoing it is obviously necessary to re-define the Family of the Proteocephalidae, since the definition of La Rue is not adapted to include such forms as *Monticellia* (which La Rue places in a distinct family), *Rudolphiella* and *Marsypocephalus*. The definition must also take into account the definitions of the other two families of the Order, viz. the Onchobothriidae and Phyllobothriidae. The Family Proteocephalidae may be re-defined as: Tetraphyllidea, with scolices unarmed or armed with small hooks or spinelets, with four sessile suckers devoid of areola or accessory suckers. An apical organ is frequently present and occasionally a distinct muscular rostellum. Vitellaria lateral, follicular, the follicles usually being closely grouped about a central duct, when in the medulla, but, when situated in the cortex, spread

[1] This should be named *P. bengalensis* (Southwell): *vide* Woodland, 1925 *b*.

out over a relatively broad lateral area. Ovary bi-lobed and posterior. Uterus with lateral diverticula and one or more median ventral uterine openings. Vitellaria, testes, ovary and uterus usually within the inner longitudinal muscle sheath but in certain genera one or more of these organs may be situated in the cortex. Habitat: intestines of fresh-water fish, Amphibia and Reptiles.

In conclusion I wish to express my indebtedness to Dr F. E. Beddard, F.R.S., for the kind loan of Schwarz's Inaugural Dissertation on "Die Ichthyotaenien der Reptilien" (Basel, 1908), and to Mr B. K. Das, M.Sc., and Mr Satkori Datta, M.Sc., of the Allahabad University, who kindly gave me much assistance in collecting the Cestode and other parasites from the local fauna.

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(*MS. received for publication* 20. v. 1925.—Ed.)

Postscript (*July 7th,* 1925):—Since the preceding was sent to press, I have received a copy of Fuhrmann's paper on the Cestoda of the Third Tanganyika Expedition (*Proc. Zool. Soc. London,* 1925, p. 79). Here I can only note the facts that Fuhrmann now regards his previous genus *Rudolphiella* as synonymous with Diesing's *Ephedrocephalus,* and that his new genus *Loennbergia* is synonymous with Wedl's *Marsypocephalus* (*vide* Woodland 1925 *a*).

W. N. F. W.

A NEW SPECIES OF *MONOPYLIDIUM, M. CHANDLERI,* FROM THE RED NETTLED LAPWING (*SARCOGRAMMUS INDICUS* STOLICZKA), WITH A KEY TO THE SPECIES OF *MONOPYLIDIUM.*

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(*From the Hook-worm Research Laboratory, School of Tropical Medicine, Calcutta.*)

(With 4 Text-figures.)

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I. Description of *Monopylidium chandleri* n.sp.

This worm was obtained from the intestine of *Sarcogrammus indicus* Stoliczka at Nagpur, C.P., India. It was flattened out between two glass slides, fixed in Mann's fluid and stained with Delafield's haematoxylin. The measurements of the worm given in the following description relate to the flattened specimen.

The worm is 70 mm. long, consisting of about 135 well-defined segments. Behind the head there is a broad unsegmented neck region, about 2–2·5 mm. in length, measuring from the level of the suckers, but the first indications of segmentation are so obscure that it is impossible to state exactly where it begins. All the proglottides are wider than long. The mature proglottides are about 0·46 mm. long and have a maximum width of 1·4 mm. The gravid segments are 0·7–0·79 mm. long with a maximum width of 3·3 mm.

The scolex is not distinctly set off from the neck, and has the same diameter as the latter, about 0·92 mm. The unarmed suckers are slightly oval and measure 220μ and 260μ in diameter.

The large muscular rostellum (Fig. 1) is of a conical shape ending anteriorly in a rounded knob. It measures 517μ in length with a maximum width of 320μ. It bears 20 hooks, the alternate ones of which are set on different levels; it is largely a matter of definition whether or not such an arrangement should be considered a single or a double row. Both sets of hooks are of the

same length and of the same shape. They measure 117μ long. Each hook (Fig. 2) has a short blade, 46μ long, a long root curving slightly upwards at its anterior end and a guard sometimes slightly enlarging distally. The distance from the end of the guard to the outer curvature of the hook is from 32μ to 34μ.

There are only 14–15 segments in which well-developed genitalia (not considering the uterus) could be made out.

The testes (Fig. 3, *t.*), 20–24 in number, are more or less spherical and are about 90μ in diameter. They are posterior to the ovary, except a few on the poral side which are lateral to it. The vas deferens (*v.d.*) is a loosely-coiled

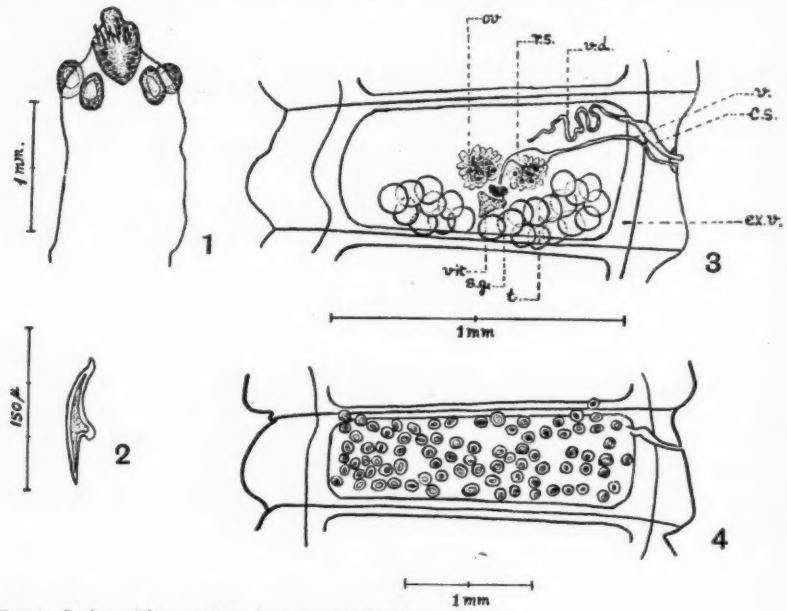

Fig. 1. Scolex with a portion of unsegmented region. ×20.
Fig. 2. A hook on the rostellum. ×160.
Fig. 3. A mature proglottis. ×44.
c.s. cirrus-sac; *ex.v.* excretory vessel; *ov.* ovary; *r.s.* receptaculum seminis; *s.g.* shell gland; *t.* testes; *v.* vagina; *v.d.* vas deferens; *vit.* vitelline gland.
Fig. 4. A gravid proglottis. ×20.

tube in the anterior region of the proglottis opening at the base of the cirrus-sac. The cirrus-sac (*c.s.*) is long and narrow and measures 176μ in length. In some segments the cirrus is everted beyond the genital opening, the longest eversion measuring 16μ in length.

The genital openings are irregularly alternate and present the following sequence: LLLRLLLRLRRRLLLR. They are situated a little anterior to the middle of the proglottis margin. Surrounding the genital opening there is a small genital atrium.

The ovary (Fig. 3, *ov.*) is situated centrally in the segment and consists of two lobes which are approximately equal. The vagina (*v.*) is a straight tube posterior to the vas deferens. After it reaches the region of the poral lobe of the ovary, it enlarges into an oval receptaculum seminis (*r.s.*) which measures about 117μ in length and 75μ in width. At the median end of the receptaculum seminis the vagina again becomes a narrow tube and passes posteriorly below the lobes of the ovary to the shell-gland (*s.g.*), which lies in the angular space between the ovary and the vitelline gland (*vit.*). The latter is smaller than the lobes of the ovary and is roughly triangular in shape, though somewhat variable.

The outlines of the developing uterus could not be followed in the region behind the sexually mature segments but in the last 59 segments there are scattered egg-capsules, about 140–165 in number, with no trace of a uterus sac. Each capsule contains only a single egg (Fig. 4). The eggs are spherical, the diameter being 82μ and of the contained embryo 48μ.

A single set of reproductive organs in each proglottis, armed rostellum, genital pores irregularly alternating and the fact that the uterus breaks down into egg-capsules each containing a single egg, place this worm in the genus *Monopylidium* as defined by Ransom (1909).

II. Systematic position of *Monopylidium*.

The genus was founded by Fuhrmann (1899) with *M. musculosa* as the type species. It is very closely related to the genus *Choanotaenia*, being in fact separated from it by the character of the uterus: in *Choanotaenia* the latter is persistent and sac-like, but may be subdivided into numerous, small communicating chambers incompletely separated by partitions, infolded from the wall of the uterus, so that, in most cases, the eggs appear almost as if isolated in the parenchyma; while in *Monopylidium* the uterus is strongly branched and finally breaks up into egg-capsules, each containing a single egg. Braun (1900) included these two genera in the sub-family Dipylidiinae Raill., whereas Fuhrmann (1908 *a*) placed them in two separate sub-families: *Monopylidium* was placed in the sub-family Dipylidiinae Raill. along with *Dipylidium*, *Oochoristica*, *Pancerina* and *Polycoelia*, while *Choanotaenia* was placed in the sub-family Dilepiinae along with various genera among which were *Lateriporus*, *Dilepis* and *Cladotaenia*. Ransom (1909) doubts the justification for retaining *Monopylidium* and *Choanotaenia* as separate genera, much less as representatives of two separate sub-families, but Lühe (1910) creates a new genus *Parachoanotaenia* for Fuhrmann's genus *Choanotaenia* and retains the latter name for species in which the uterus breaks up into egg-capsules but in which there is a single crown of hooks, whereas he restricts *Monopylidium* to species with a double crown of hooks. However, as suggested above, there seems to be no clear demarcation between forms with single and double rows of hooks. In the case of the species here described, for instance, where all the hooks are of the same size and shape, but in which the alternate

ones are set at slightly different levels on the rostellum, it is merely a matter of opinion whether or not they should be considered as being arranged in one or two rows. It seems impractical, therefore, to retain Lühe's two genera and, for the present, it seems preferable to retain the name *Choanotaenia* for forms with a persistent uterus.

III. Diagnosis of *M. chandleri* n.sp.

As the species described in this paper differs from any other species of *Monopylidium*, I consider it a new species for which I propose the name *M. chandleri* with the following specific characterisation: Length of the worm 70 mm., with a maximum width of 3·3 mm.; 20 hooks on the rostellum, alike in size and form but alternate ones set on slightly different levels; rostellum large, 517μ long with a maximum width of 320μ, not distinctly set off from the neck; neck broad, 2–2·5 mm. long; scolex 0·92 mm. wide; proglottides all wider than long; testes 20–24, posterior to ovary but a few extending laterally to it on the poral side; diameter of testes 90μ; receptaculum seminis present, 117μ long and 72μ wide; uterus breaks up into egg-capsules each containing one egg; diameter of the egg 82μ and of the contained embryo 48μ. Habitat—intestine of *Sarcogrammus indicus* Stoliczka. Locality—Nagpur, C.P., India.

IV. *Southwellia* n.g. and *Macracanthus* n.sub-g.

All the species of *Monopylidium* hitherto described, with the exception of *M. gallinarum* Southwell 1921, although showing a very wide range in the number and size of hooks and in the total length and width of the worm have the following characteristics in common: Head with unarmed suckers and large rostellum, bearing 14–40 hooks which vary in size in different species from 15μ to 148μ. Neck absent or short; ovary bi-lobed (except in *M. fieldingi* Maplestone and Southwell, 1923). Testes from 16–40 in number varying in size from 40μ to 90μ in diameter and situated behind the ovary. Vagina with a well-developed receptaculum seminis. Genital pores irregularly alternate and situated a little in front of the middle of the edge of the proglottis. Uterus breaks down into egg-capsules, each containing a single egg, except in *M. unicoronata* Fuhr. (1908 *b*) and *M. musculosa* Fuhr., though two or three or more eggs described in the egg-capsules of these two species may be due to examination in imperfectly ripe proglottides, since such proglottides, as Maplestone and Southwell (1923) have pointed out, have at first numerous eggs in capsules, the eggs being isolated only with the complete ripening of the proglottides. It would be observed that *M. gallinarum* Southwell 1921 differs from all the other species of *Monopylidium* in the following important combination of characters: Very numerous (120) large hooks (90μ in length), small-sized testes (35μ in diameter), some of which are situated in front of the ovary, unilateral genital pores, situated at the extreme anterior corners of the segments, and in the fact that there are five to nine eggs in each capsule. Since Southwell himself (Maplestone and Southwell, 1923) calls attention to

the fact that several eggs are found in capsules in imperfectly ripe proglottides and yet gives this as a character of this species, it may be assumed that he is speaking of fully ripe proglottides. For these reasons it seems advisable to separate *M. gallinarum* Southwell 1921 from the other species of *Monopylidium* and to establish for it a new genus for which I propose the name *Southwellia* in honour of the discoverer of the species. It is possible that *M. rostellata* Fuhr. 1908 from *Himantopus mexicanus*, in which the hooks are lost, but in which the genital pores are described as unilateral, may be found to be co-generic with *M. gallinarum* Southwell 1921. For the genus *Southwellia*, I propose the following generic diagnosis:

Hooks very numerous (120) and of large size (90μ), arranged in two rows; rostellum small and bluntly pointed. Neck absent; genital pores unilateral, situated in the extreme anterior corner of the segment. Cirrus-sac large and muscular; genital atrium present; testes of small size situated lateral to and in front of the ovary; uterus breaks down into egg-capsules each containing five to nine eggs.

M. macracanthum Fuhr. 1908, as described by Maplestone and Southwell (1923) from specimens obtained from *Lobivanellus lobatus* Lath., differs somewhat from Fuhrmann's description (1908 *c*). Fuhrmann's worm has 22 hooks, the width of the scolex is 720μ, and it has "many" eggs. In contrast to this, Maplestone and Southwell's specimens have 26 hooks, the width of the scolex is 600μ and the number of testes is 23–30, besides the whole worm being larger and narrower. On further examination, it may, perhaps, be found out that Maplestone and Southwell's specimens represent a new species.

There are three species of *Monopylidium*, viz. *M. stercorarium* Baylis (1919), *M. macracanthum* Fuhr. (1908 *c*) and *M. chandleri* here described which have a small number (14–26) of very large hooks. In the other species, the lengths of hooks range from 15μ to 54μ and, therefore, the species mentioned above with hooks ranging from 110μ–148μ in length form a group by themselves. I suggest, therefore, that these three should be included in a new sub-genus for which I propose the name *Macracanthus*.

In the following key, two species of *Monopylidium* have been left out: *M. rostellata* and *M. musculosa*. The former is described from a specimen in which the hooks were lost and it has unilateral genital pores: it positively cannot be retained, therefore, in the genus *Monopylidium*. The original description of the latter species was not available to me.

In conclusion, I desire to express my gratitude to Dr Asa C. Chandler, in charge of the Hook-worm Research, for very valuable help and guidance.

V. Key to the species of *Monopylidium*.

1 (8) (15) Size of hooks less than 25μ 2

2 (7) Number of testes less than 25 3

3 (6) Number of hooks 30 4

4 (5) Length of body 7 mm.
Maximum width 0·79 mm.. length of hooks 19μ: width of scolex 300μ; testes 22, 54μ in diameter . . . . . *secundum* Fuhr. 1908

5 (4) Length of body 35 mm.
Maximum width 0·5 mm., length of hooks 15μ; width of scolex 240μ; testes 20
arcticum Baylis 1919

6 (3) Number of hooks 40
Length of body 50 mm., maximum width 1·2 mm.; length of hooks 22μ; width of scolex 400μ; testes 16–21; ovary trilobed
fieldingi Maplestone and Southwell 1923

7 (2) Number of testes 30
Length of body 30 mm.; maximum width 0·75 mm.; length of hooks 14–16μ; width of scolex 160μ; testes 50μ in diameter . . . *passerinum* Fuhr. 1908

8 (1) (15) Size of hooks more than 25μ but less than 60μ 9

9 (14) Number of hooks less than 25 10

10 (13) Breadth of scolex 350μ or less 11

11 (12) Diameter of testes 40μ
Maximum width of body 0·5 mm.; 22 hooks, each 54μ long; width of scolex 350μ; testes 18–20 . . . . . *cayennense* Fuhr. 1908

12 (11) Diameter of testes 68μ
Maximum width of body 0·8 mm.; 22 hooks, each 48μ long; width of scolex 290–300μ; testes 20–24 . . . . . *unicoronata* Fuhr. 1908

13 (10) Breadth of scolex 450μ
Length of body 10–20 mm.; maximum width 0·8 mm.; 16–18 hooks, each 43μ long; testes 20, 60μ in diameter . . . . . *sorcinum* Cholod. 1906

14 (9) Number of hooks more than 25
Length of body 40 mm.; maximum width 1 mm.; hooks 28–35, each 25–31μ long; width of scolex 340μ; testes 20–24 *crateriformis* (Goeze 1782) Clerc. 1902

15 (1) (8) Size of hooks 110μ–148μ (sub-genus *Macracanthus*) 16

16 (17) Number of hooks 14
Length of body 25–30 mm.; maximum width 0·8 mm.; length of hooks 110μ; width of scolex 400μ; testes 40 . . . . . *stercorarium* Baylis 1919

17 (16) Number of hooks more than 14 18

18 (19) Hooks of one size only
Length of body 70 mm.; maximum width 3·3 mm.; hooks 20, each 117μ long; width of scolex 924μ; testes 20–24, 90μ in diameter . . . *chandleri* n.sp.

19 (18) Hooks of two sizes
Length of body 25–30 mm. (Fuhr.) or 45 mm. (Maplestone and Southwell); maximum width 2·5–3 mm. (Fuhr.) or 1·8 (Maplestone and Southwell); long hooks 148μ or 145μ; small hooks 110μ; width of scolex 720μ (Fuhr.) or 600μ (Maplestone and Southwell); testes "many" (Fuhr.) or 23–30 (Maplestone and Southwell) . . . . . *macracanthum* Fuhr. 1908

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(*MS. received for publication* 27. IV. 1925.—Ed.)

N. A. CHOLODKOVSKY
1858—1921

Separate copies may be obtained from the University Press, Cambridge

NOTES ON THE LIVES OF CHOLODKOVSKY AND PORTCHINSKY.

(With Portrait-plates 31 and 32.)

By E. N. PAVLOVSKY, M.D., D.Sc.
Professor of Zoology, Military Academy of Medicine, Leningrad.

N. A. Cholodkovsky.

1858–1921.

(Portrait-plate 31.)

N. A. Cholodkovsky was born on the 4th of March 1858 at Irkutsk, Siberia, where his father was a physician. He attended school in St Petersburg (now Leningrad) and at the age of 17 entered the Academy of Medicine. After completing his medical education, having no inclination for practice, he joined the University and in 1885 obtained the lectureship of Zoology in the Institute of Forestry.

In 1892, he obtained the doctor's degree in zoology and the chair of zoology in the Military Academy of Medicine which he occupied until his death, April the 2nd 1921. Although mainly interested in entomology, Cholodkovsky also studied various parasitic worms and especially the Tape-worms. He founded a very large collection of parasitic worms, containing more than 1000 specimens, now preserved in the Academy of Medicine.

In 1899, Cholodkovsky published the first atlas of worms parasitic in man (*Icones helminthorum hominis*), containing numerous excellent original figures. Of his published papers, numbering about 180 in all, 30 deal with parasitic worms. In his entomological investigations Cholodkovsky gave much attention to parasitic insects such as fleas, bugs, lice and bot-flies, but specially to those parasitic on plants: Aphidae and Chermesidae. In this field he made most important investigations which will always remain associated with his name and most of which are incorporated in his well-known monograph on Chermesidae.

Cholodkovsky is also known in Russia as the author of excellent text-books of zoology, comparative anatomy, and pure and applied entomology. During his life he succeeded in creating a real school for parasitological investigation and has left several pupils who are actively engaged in this branch of study.

In spite of his great contributions to science, scientific work did not absorb all his activities, for he devoted much time to literature. In this field, as in science, he attained some celebrity. Cholodkovsky is known in Russia as the best translator of Goethe's *Faust*, a translation which ran through eleven editions. He also translated poems of Byron, Milton, Shakespeare, and others into Russian verse. Cholodkovsky wrote many original poems which

remained unpublished during his lifetime. After his death a booklet of short poems, delightfully and vividly describing different flowers, appeared under the title *From the Herbarium of my Daughter*.

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J. A. Portchinsky.

1848–1916.

(Portrait-plate 32.)

J. A. PORTCHINSKY was born on the 9th of February 1848 in the village of Svatova Lutchka (Province of Kharkov), his father being an army surgeon. After leaving school he studied in St Petersburg University, at the Natural History Department, where he began his zoological work under Prof. K. Kessler. In 1875, Portchinsky obtained a post at the Ministry of Agriculture where he served for the remainder of his life. He organised the Bureau of Applied Entomology and later became its chief. He dedicated his whole life to entomological work and was intimately connected with the Russian Entomological Society, of which he was secretary for 22 years. He died 11th May 1916 in Petrograd.

He travelled extensively in Russia and in Siberia studying local pests not only of agricultural plants but also of domestic animals and of man. His main speciality was the biology of insects but he devoted also considerable time to systematics. Most of his work concerned the biology of Diptera, notably that of *Wohlfartia*, *Sarcophila*, *Sarcophaga*, *Cynomyia*, *Stomoxys*, *Lyperosia*, *Haematobia*, *Musca*, *Pyrellia*, *Lucilia*, *Fannia*, *Gastrophilus*, *Oestrus*, *Rhinoestrus*, and others. In a long series of papers, 124 in number, Portchinsky published several important monographs vividly written and richly illustrated. He described a number of new species of Tabanidae and of the genera *Wohlfartia*, *Portchinskia*, *Oestromyia*, etc. He studied also vine *Phylloxera*, *Cecidomyia*, and many other injurious insects and their parasites. Certain of his papers dealing with folklore and popular superstitions connected with insects are of interest.

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J. A. PORTCHINSKY
1848—1916

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A NEW CILIATE, *CHARON VENTRICULI* N.G., N.SP., FROM THE STOMACH OF RUMINANTS.

By A. PRINGLE JAMESON.
Institute of Animal Pathology, Cambridge.

(With 1 Text-figure.)

In the course of the examination of the contents of the paunch and rumen of 70 Ruminants a Ciliate of an interesting type has been met with on eight occasions. It is surprising that a new form should be found in this situation as a number of workers seem to have devoted no little time to researches on the fauna of the ruminant stomach. One cannot think that this animal is to be found only in England, and we are driven to the conclusion that it must have been overlooked up to the present. As the organism is relatively small for a Ciliate and of a rather transparent appearance this is understandable, especially because it is rarely abundantly present. Although it has been found eight times, yet in a coverslip preparation where there will be several specimens of the other Ciliates in every field of the microscope, there may not be more than one or two specimens of this new form.

Despite the rather slight infections found, this form may readily be picked out from the bustling crowd of other organisms present in the stomach-contents by its method of locomotion. This is regular and not very rapid, and seems to be accomplished mainly by two prominent tufts of cilia, which are situated very near the posterior end of the body. The anterior end of the body is covered with many cilia and among these there can be made out two tufts of cilia, similar to the posterior pair but less prominent. The anterior pair, while evidently also locomotory, seem to be less important than the posterior tufts. These move in unison with slow, somewhat jerky strokes, producing a motion suggestive of a badly rowed boat. This method of progression is so characteristic that I have given the name *Charon* to this new genus. For a specific name I propose that of *ventriculi* in recognition of the position in which the parasite is found.

The length of the body varies between 24 and 36μ and the breadth between 12 and 15μ. Typically it is more than twice as long as it is broad. It is very much compressed dorso-ventrally, so that seen from the side—a rare view however—it is very narrow, about 3μ in thickness. The shape resembles somewhat the blade of a lancet, one side being convex while the other is nearly straight. The anterior end is bluntly pointed and, especially in stained specimens, gives the impression of being pinched into a projecting knob. The

posterior end tapers to a finer point than does the anterior, but it is also rounded, and in stained specimens it has a slightly pinched appearance. The ventral surface is flat or very slightly concave; the dorsal surface is very slightly convex; the right side is straight; the left side is convex.

The arrangement of the cilia has already been mentioned. The two pairs of ciliary bundles are characterised by their stiff, long cirri, which are capable of bending only towards the tips. The two posterior bundles lie one on each side of the body very close to the end and each is inserted in a roundish oval socket. In moving the whole bundle moves as one. The anterior bundles are very much the same as the posterior ones but the cirri are shorter and they are less compactly grouped. They are placed one on each side of the body, at the base of the anterior knob and on a level with the mouth. The whole of the anterior projecting tip is covered with cilia and it is not always easy to distinguish the anterior bundles from the rest of the anterior cilia. These

Charon ventriculi from the ventral side. × 1500.
(From a stained specimen.)

latter are more flexible than the cirri and they move in a rather scrambling fashion, seemingly concerned with the gathering of food towards the mouth.

The mouth is placed on the ventral surface of the body, immediately posterior to the anterior ciliated tip; indeed, the hindmost cilia form a fringe to the anterior lip of the mouth. The mouth-opening is round or slightly pear-shaped and lies to the right side of the body. In stained specimens the mouth seems to be projecting slightly from the ventral surface, as if raised on a low cone, but this appearance is not visible in fresh specimens and it is possible that it is mainly the effect of fixatives.

The mouth opens at once into a prominent pharynx, which extends deep into the body, reaching at least half-way to the posterior end, and curving slightly to the right. It narrows towards its end, which is lost in the granular endoplasm. Attached to the left side of the pharynx is a well-developed ciliary membrane, made up of stout little cirri, which seem to be fixed together

so that they act as a sort of undulating membrane. This organ extends the whole length of the pharynx. The food consists of bacteria and fine organic particles. There is no permanent anal opening, but occasionally a temporary anus can be seen opening at the extreme posterior tip of the body. A single large contractile vacuole lies in the posterior part of the body, expanding and contracting very deliberately.

There is a large round macronucleus, which varies in its position in the body, but is most commonly found about the middle, lying near the end of the pharynx. The structure of this nucleus is coarsely granular. The micronucleus is oval in shape and may lie in a depression in the macronucleus or may be some little distance from the latter.

The shape of the body is constant, being bounded by a very delicate cuticle with a thin underlying layer of ectoplasm. The endoplasm is finely granular and transparent.

Division was observed on several occasions and was of the usual ciliate type, a new pharynx being formed in the posterior portion while division was proceeding. Conjugation was not observed.

C. ventriculi was found in seven cattle and in one sheep.

Charon ventriculi undoubtedly is most closely related to the genus *Blepharocorys* Bundle (1895), but it is more simply organised than the members of that genus. It is true that it does not appear to have many points in common with the three species described by Bundle, but if we consider Schumacher's (1915) excellent account of *Blepharocorys equi* it will be seen that there are certain affinities between the two. The complex anterior casque of *Blepharocorys* is represented in *Charon* by the simple anterior projection. The prominent depression in which the mouth of *Blepharocorys* opens is absent in *Charon*. There is no sign in *Charon* of the anal opening which is so clearly seen in the other genus. The arrangement of cilia in the two genera is roughly the same, an anterior group and a posterior group, but in *Charon* the posterior cilia are in two compact bundles, while in *Blepharocorys* they form a single rather scattered group; the anterior cilia are more alike, but here again the arrangement seen in the new genus is more precise and compact than in the old. A further point of interest to note is the habitats of the two genera—one being found in the caecum of the horse while the other is found in the paunch and rumen of cattle and sheep.

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(*MS. received for publication* 22. VI. 1925.—Ed.)

A NOTE ON THE CILIATES FROM THE STOMACH OF THE MOUSE DEER (*TRAGULUS MEMINNA* MILNE-EDWARDS) WITH THE DESCRIPTION OF *ENTODINIUM OVALIS* N.SP.

By A. PRINGLE JAMESON.
Institute of Animal Pathology, Cambridge.

(With 1 Text-figure.)

Through the kindness of my friend Mr Clifford Dobell, F.R.S., I have come into the possession of a quantity of preserved stomach-content from the Mouse Deer of Ceylon (*Tragulus meminna* Milne-Edwards). As there are no descriptions, so far as I can find, of the Ciliates from Asiatic Ruminants, it seems worth while to publish a brief note on the organisms found in this material.

The presence of Ciliates in the stomach of the Mouse Deer was observed by Dr A. Willey, F.R.S., who drew Mr Dobell's attention to them. Two of these animals were obtained from the jungle and both were found to be heavily infected. These facts have been recorded in *Spolia Zeylanica* by Dobell (1910). The material was collected on the 2nd of August, 1909, and consists of three coverslip smears fixed in Schaudinn's fixative and stained with Delafield's haematoxylin—these have been re-stained with Heidenhain's iron haematoxylin—and a quantity of stomach-contents fixed in bulk in Schaudinn's fixative, bichromate-acetic, and 40 per cent. formaldehyde, the last not being very satisfactory. This bulk material has been centrifuged to separate out the vegetable matter as much as possible, and stained in bulk, some in Weigert's iron haematoxylin and some in paracarmine. It has been mounted in Euparal or in absolute alcohol balsam. The material is labelled "stomach-contents," but it undoubtedly was from the paunch only.

It was hoped that, coming as it did from a jungle-inhabiting animal and not from a domesticated, stall-fed creature, the fauna in the paunch might show some new and perhaps striking forms, but on the whole it has proved to be extraordinarily like that of our European domesticated Ruminants. There are no new genera to be reported and only one new species. It is interesting to note, however, that certain of the species show slight differences from their European representatives.

Members of three genera have been found. Most numerous are representatives of the genus *Entodinium*. These are nearly equalled in numbers and

surpassed in prominence by the closely-related genus *Diplodinium*. The genus *Isotricha* is also present although not so abundantly as the other two.

Genus *Entodinium*.

It is unfortunate, to say the least of it, that practically all the specific differences described in this genus are founded on the external contours of the body, so that, unless we are dealing with species with strongly marked features like those of *E. rostratum* or *E. caudatum*, it is not easy to say where one species begins and another ends. If only a little more attention had been paid to the internal features of the organisms, much of this difficulty might have been removed. The species of *Entodinium* which are present in my material are to be referred to the less well-defined members of the genus, *E. bursa* Stein and *E. dubardi* Buisson. The examination of a very large amount of material from British Ruminants has led me to the belief that these two species, with perhaps the addition of *E. minimum*, are linked by a series of intermediate forms so that they probably should be regarded as varieties of one species, *E. bursa* Stein. As I hope to develop this point in a future paper I shall not do more than refer to it here and continue to use the old specific names for the present.

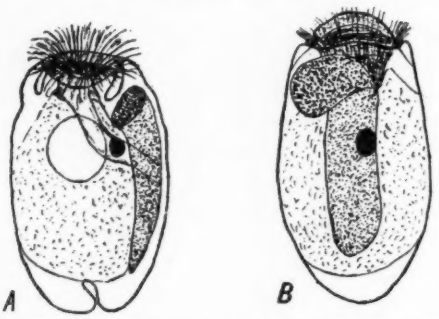
The most abundant representative of the genus is *E. dubardi* Buisson. This species was described by Buisson (1923 *a* and *b*) from preserved material and in consequence the descriptions are not as convincing as they might otherwise have been, nor are the figures very illuminating. If we take the relatively large ectoplasmal expansions of the sides and the prominent anal canal as the characteristic features of the species, it is possible to distinguish a considerable number of forms of this type. The nucleus in these is not quite of the type described by Buisson. It is much larger, occupying the whole length of one side, and as a rule it does not taper to a point. In addition no striping could be detected on the cuticle. Some forms closely resembling *E. bursa* Stein are also present. These call for no comment beyond the observation that the nucleus is more prominent—altogether bigger—than in European specimens. A number of intermediate forms which might be placed in either species are also to be seen.

Description of a new species, *E. ovalis*.

In addition to the above there are some organisms which seem to me to be different from any of the other members of this genus. For these I propose the name *Entodinium ovalis*, but as I have not had the opportunity of observing the animals alive I put this forward as a new species with the reservation that the description must consequently be incomplete. The most characteristic feature of this species is the absence of dorso-ventral flattening. In consequence, when looked at from either end, the outline is very nearly circular—rounded oval to be exact. The animal is small, measuring from 20 to 40μ in length by from 12 to 20μ in width, the thickness being rather less, 10 to 18μ. The

posterior end is bluntly rounded and is composed of ectoplasm only. A short, nearly vertical anal canal runs through this into the endoplasm. The anterior end is truncated as in all members of this genus, but only slightly obliquely, and when the wide mouth-opening is contracted the anterior end is markedly rounded. This rounding is caused by the lips, which close the mouth, being very stoutly built, so that when they come together they form a broad dome-shaped prominence at the anterior end.

The pharynx, which leads from the mouth into the endoplasm, is long and curves to the left and dorsally. The macronucleus is very large, being both long and broad, and is actually longer than the body so that it is bent at the anterior end into a right-angled hook. The micronucleus is round or round oval and lies as a rule to the inner side of the macronucleus and towards its anterior end. Occasionally a vacuole is seen on the ventral side of the body towards the middle in the anterior half; this is doubtless the contractile



E. ovalis n.sp. × 1500. *A*, ventral view; *B*, lateral view.

vacuole. The name *ovalis* is proposed for this form on account of its characteristically oval outline as seen from any side.

As has been remarked, the nucleus in all species of this genus found in the Mouse Deer is very large. I am unable to account for this peculiarity, but it is so striking that it deserves to be specially emphasised.

Genus *Diplodinium*.

The most prominent species is *D. ecaudatum* Fiorentini. This is present in five of the forms described by Sharp (1914)—*ecaudatum*, *caudatum*, *bicaudatum*, *tricaudatum* and *quadricaudatum*. Of these the first three are the most abundant. The forms seen in this material are not quite typical. They are built much more squarely, especially at the posterior end, and the spines, where present, are much shorter and more acutely pointed, more compressed and more fragile, more thorn-like than spine-like, than one usually finds in similar varieties from European Ruminants. *D. bursa* Stein is also common and corresponds exactly with the published descriptions. A third species, *D. magii* Fiorentini, is present but is not abundant. All the specimens are

large and are distinguished by the number of contractile vacuoles, six being a common number. The macronucleus is also very prominent and while it conforms to the general pistol shape so characteristic of this species, the handle-like portion at the anterior end is strongly developed and is usually bent into a nearly closed loop.

Genus *Isotricha*.

Isotricha intestinalis Stein is present in fair numbers and beyond the observation that the shape is markedly more rounded—practically round in many cases—than is usually found in this species, there is nothing worthy of remark in the specimens in my preparations.

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(*MS. received for publication* 22. VI. 1925.—Ed.)

A STRONGYLOID NEMATODE, *WARRENIUS BIFURCATUS* N.SP., FROM THE RICHARDSON GROUND SQUIRREL.

By GEORGE F. SLEGGS, B.Sc.

(*University of Saskatchewan.*)

(With 9 Text-figures.)

The genera *Citellinema* and *Warrenius* were established by Hall in 1916 with regard to specimens collected from alcoholic host material supplied by Mr E. R. Warren. The genus *Citellinema* was founded upon a single male specimen from *Citellus elegans*, named by Hall *Citellinema bifurcatum*, in reference to the bifurcated spicules. The genus *Warrenius* was based upon two males, one headless, from *Eutamias quadrivittatus*, to which Hall gave the name *Warrenius quadrivittatus*.

The present writer has had the opportunity of examining preserved material of *Citellus richardsonii*, the common ground squirrel of Saskatchewan, and has secured an abundant amount of both sexes of a strongyloid nematode which, on the advice of Mr Hall, to whom he forwarded specimens for examination, he is designating a new species of the genus *Warrenius*.

I propose to term the species *W. bifurcatus*. On first examination it seemed that the species must be a *Citellinema*, since the spicules are bifurcated deeply, the bifurcations being in different planes, exactly as figured by Hall for *C. bifurcatum*. The bursa, however, resembles that of *Warrenius*; and the simple head, with its unilateral wing, agrees with the head of *Warrenius*, and differs from the head of *Citellinema*, in which the cuticle is raised up into a collar and lacks the cervical wing. The absence of the pronounced longitudinal striation of the cuticle of the bursal rays furnishes another difference from *C. bifurcatum*. Hall was unable to determine the nature of the dorsal ray of *C. bifurcatum*, and this also was found to resemble, in its dichotomous branching (though not in the relative lengths of the branches), *W. quadrivittatus*. There seems to be no doubt, therefore, that the species under description in this paper belongs to the genus *Warrenius*, although the agreement of the spicules with *Citellinema bifurcatum* is remarkable. The parasite falls in the family Trichostrongylidae Raillet, 1915, and the subfamily Trichostrongylinae Leiper, 1908.

Generic diagnosis. Warrenius. Head simple, no lips evident. Cuticle of head inflated, with a unilateral cervical wing. The bursa is deeply incised

dorsally to form two large lateral lobes, and a small dorsal lobe. The dorsal, lateral, and ventral ray systems are well defined and separated from one another, the rays of each system being more closely related to one another than to the rays of other systems. The dorsal lobe is supported by the dorsal ray which branches dichotomously[1]. The externo-dorsal rays are slender wavy rays lying in the lateral lobes, the tips of which are some distance from the bursal margin. The recurved tip turns towards the dorsal ray and is closer to this than to the postero-lateral. The postero-lateral and medio-lateral rays originate in a common stem. The latero-ventral and ventro-ventral rays originate as branches of a thick common stem and diverge from their origin to their termination near the bursal margin. They are unusually large for ventral rays. The spicules are long. Uteri divergent, the vulva in the posterior half of the body. Ovijectors developed.

Description of the Species.

The worms are whitish in colour. The male is considerably shorter and not so stout as the female, and may exhibit two or three flat coils, or may be coiled in a flat spiral. The female is very strongly coiled, in an elongated spiral (Fig. 1), the extremities of the body being frequently hidden within the ends of the coil. The posterior extremity of the female bears a minute, curved, cuticular spine.

The cuticle is finely striated transversely and presents also a number of thicker longitudinal striae, numbering about 24, and running, at equal distances apart, from end to end of the body. Between these prominent striae are finer longitudinal striations. The cross striation of the cuticle could only be detected at the optical edge of the worm, where, however, it was very obvious.

The head is simple, there being no clear indication of lips, though in anterior view sometimes three, sometimes six, delicate radial lines were to be observed converging upon the mouth. Their exact significance has not been decided upon. The cuticle of the head is inflated, and is expanded at one side into a unilateral cervical wing (Fig. 2), near the anterior end of which is a lesser flat expansion. No buccal capsule is present.

Diameter of head in female exclusive of cuticular inflation: average 48μ.

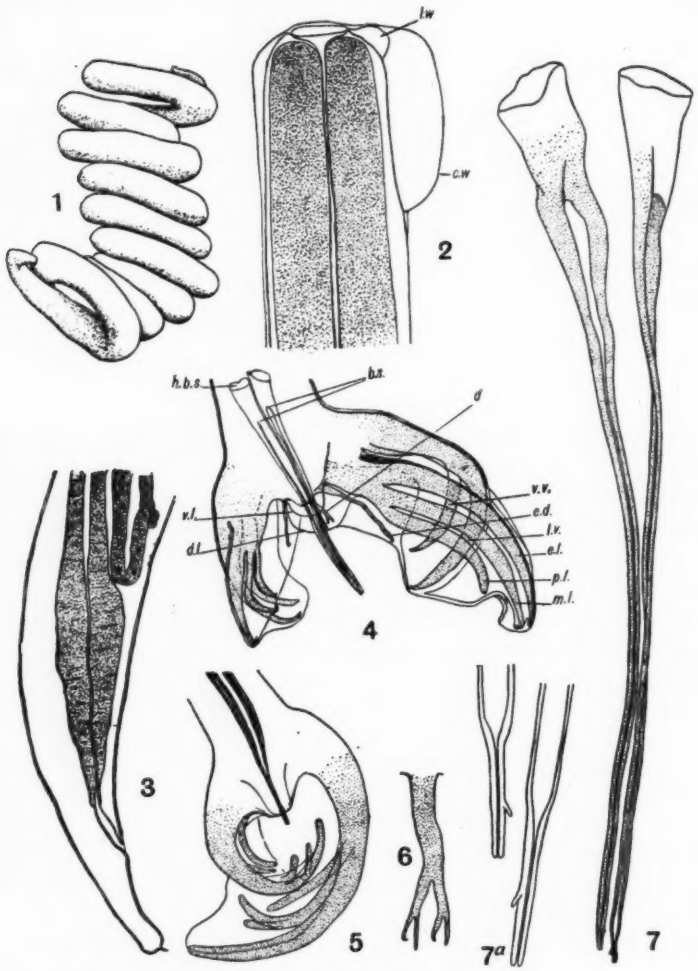
Diameter of head in male, exclusive of cuticular inflation: average 36μ.

Length of cervical wing: ranges from 52 to 92μ.

Width of cervical wing: about 25μ.

The oesophagus is longer in the female than in the male. Length of oesophagus in female about 750μ; in male, about 600μ. The oesophagus is variable

[1] The generic diagnosis given above is quoted, slightly abridged, and with modifications, from Hall, who founded the genus in 1916. Hall includes in his generic diagnosis a description of the dorsal ray which, in my opinion, is so detailed as to be more applicable to a specific diagnosis for *W. quadrivittati*, upon which he founded the genus. His description of the branches of the dorsal ray can be reduced to the statement that it branches dichotomously. Slight differences exist between *W. quadrivittatus* and *W. bifurcatus* which it seems advisable to cover by the general statement, as given above, that the dorsal ray "branches dichotomously."



Warrenius bifurcatus n.sp.

Fig. 1. ♀ in characteristic coiled attitude.

Fig. 2. Head. C.W. = unilateral cervical wing; L.W. = lesser cuticular expansion.

Fig. 3. ♀ posterior extremity, showing anus, rectum, the posterior ovary at its point of reflection, and the cuticular spine at the extreme posterior end.

Fig. 4. ♂ bursa, dorsal view. B.S. = bifurcation of spicules; D.L. = dorsal lobe; H.B.S. = hollow bases of spicules; V.L. = ventral lobe.

Bursal rays D. = dorsal; E.D. = externo-dorsal; E.L. = externo-lateral; L.V. = latero-ventral; M.L. = medio-lateral; P.L. = postero-lateral; V.V. = ventro-ventral.

Fig. 5. ♂ bursa, to illustrate overlapping of left lateral lobe by right.

Fig. 6. ♂ dorsal ray.

Fig. 7. ♂ spicules.

Fig. 7 *a*. ♂ spicules; ends, much magnified.

in length, the degree of variation amounting to as much as 15 per cent. in either sex, from the average given. The oesophagus possesses a single unicellular gland.

The nerve-ring is situated about $\frac{1}{3}$ of the way along the oesophagus, from the anterior end of the body. The oesophagus is dilated posteriorly and separated by a constriction from the mesenteron, which consists of two rows of epithelial cells, one dorsal, one ventral, free from pigment. The excretory pore is about $\frac{2}{3}$ of the way along the oesophagus.

Male. From 7 to 12 mm. long. The greatest width is near the middle of the body—215 μ. The body tapers gradually towards the anterior end. Diameter of head, exclusive of cuticular inflation, averages 36 μ. Two spicules are present (Fig. 7) each of which bifurcates about $\frac{1}{6}$ of the length from the proximal end. The bifurcation of the spicules takes place in different planes. The right spicule bifurcates in a horizontal plane, so that in dorsal or ventral view the separation of the two resulting limbs is obvious, a fairly wide space being visible between the bases of the limbs. The left spicule, however, does not show this space, the bifurcation being hardly apparent under low power, except for what appears as a line running down the middle of the spicule. Under the oil immersion this line is seen to be the edge of one of the forks of the spicule. By varying the focus it is ascertained that the left spicule bifurcates like the right, but that the plane of bifurcation is vertical, so that the two limbs are seen one above the other. The bases of the spicules are hollow and broadly campanulate.

In the bursa the postero-lateral, medio-lateral, and externo-lateral rays originate from a common stem which is united lower down with the common stem of the latero-ventral and ventro-ventral rays (Fig. 4). The externo-lateral ray is thicker at its base than the medio-lateral and postero-lateral rays with which it is associated. The two latter are approximately equal in thickness. The externo-dorsal ray is very thin, transparent and sinuous, its tip being recurved medially. The dorsal ray divides into two about $\frac{2}{3}$ of its length from its proximal end. The two branches divide into two slender sinuous terminations, whose tips are often recurved (Fig. 6). The two lateral lobes of the bursa are markedly unequal in size[1]. The right lateral lobe of the bursa is about $1\frac{1}{2}$ times longer than the left. The left lobe is usually coiled up inside the right, which bends closely over it (Fig. 5). The cuticle of the bursal rays is strongly cross striated. The cuticle is prolonged into a delicate shield which invests the spicules when exserted to half their length. It has not been possible to determine to what extent this cuticular investment covers the spicules when they are more fully exserted.

Female. Length 15 to 18 mm. Greatest width 315 to 335 μ in the region of the posterior uterus, about 1·75 mm. from posterior end. Distance of anus from posterior extremity ranges from 88 μ to 120 μ. The vulva is situated about

[1] Although the asymmetry of the bursa is indicated by Hall in his figure of *W. quadrivittatus*, he does not refer to the fact in his description.

2·6 mm. from the posterior end. The vulva is a transverse or crescentic slit. A series of convergent muscle fibres surround the vagina (Fig. 9). Muscular ovijectors, each appearing to consist of two compartments, a larger proximal and a smaller distal, are developed, and lead, by way of a slender non-muscular tube to the uteri, which possess fairly thick cuticular walls, and terminate in the ovaries. Each ovary is an elongated core of cells, which, in the distal

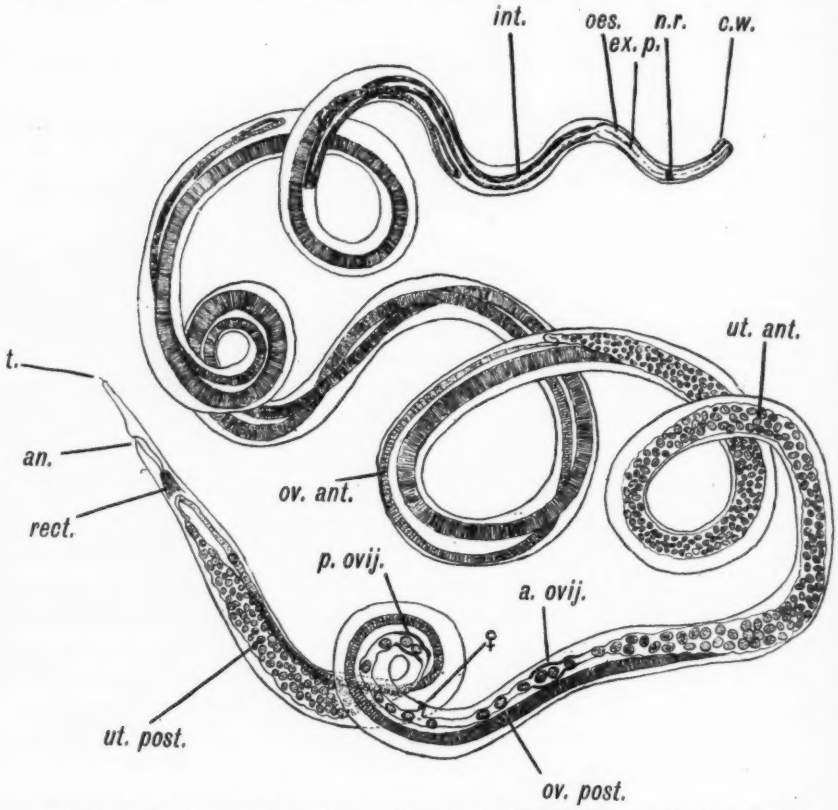


Fig. 8. *Warrenius bifurcatus* n.sp. ♀. Intestine only lightly indicated so as to show genitalia. AN. = anus; A.OVIJ. = anterior ovijector; C.W. = unilateral cervical wing; EX.P. = excretory pore; INT. = intestine; OV.ANT. = anterior ovary; OV.POST. = posterior ovary; RECT. = rectum; UT.ANT. = anterior uterus; UT.POST. = posterior uterus; T. = cuticular spine on tail; ♀ = female aperture.

portions of the ovary become very much compressed, producing a septate appearance of the ovary. Of the two divergent uteri, the posterior is the shorter, since it is limited in extent by the posterior end of the body. Hence the occurrence of the maximum body thickness in this region; since the uterus cannot lengthen, it tends to thicken. Its ovary is reflected sharply anteriorly, being thin and slightly convoluted in its proximal portion. The posterior ovary

then runs forward, increasing in thickness, for about $\frac{3}{4}$ of the body length (Fig. 8), where it thins out, and, after undergoing reflection, with one or two convolutions, it terminates. The anterior uterus is longer than the posterior, and its ovary extends farther forward, undergoing reflection in a similar manner to the posterior ovary, at a point usually twice the length of the oesophagus from the anterior extremity. The eggs are from 12- to 16-segmented, and are enclosed in thin shells. It has not been possible to figure an egg at the moment of oviposition.

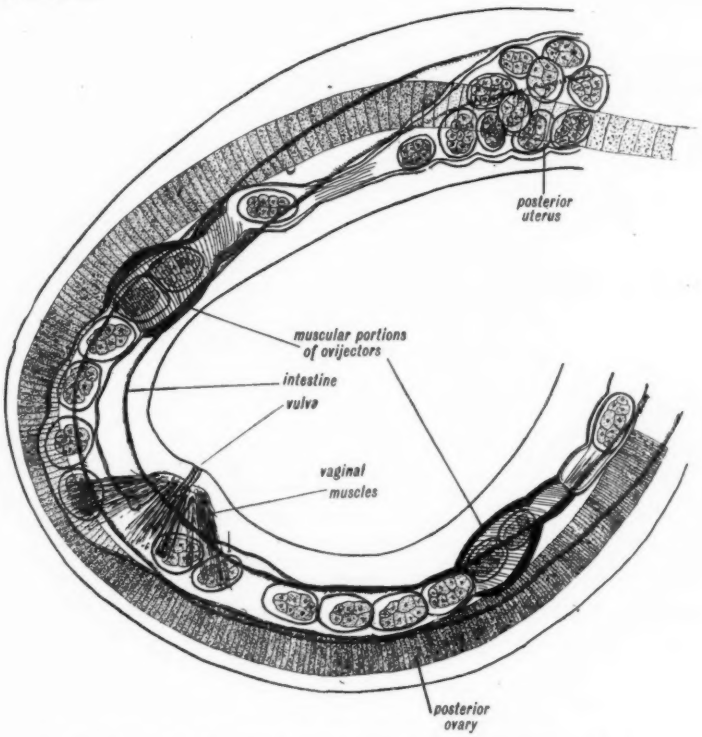


Fig. 9. *Warrenius bifurcatus* n.sp. ♀. Much enlarged view of vulval region. The edge of the intestine is cross hatched.

The parasite occurs in the anterior third of the duodenum, numbers of them being occasionally matted together, and clothed with abundant mucus.

Hall's species, *W. quadrivittati* and *W. bifurcatus* n.sp., described in this paper, may be distinguished by the following characters:

(1) In Hall's account no mention is made of bifurcation of the spicules in *W. quadrivittati*, whereas in *W. bifurcatus* they are deeply bifurcated.

(2) In *W. quadrivittati* the outer branches of the dorsal ray are very short; in *W. bifurcatus* the four branches are of equal length.

(3) In *W. quadrivittati* the cervical membrane is recurved posteriorly to form a notch; in *W. bifurcatus* the cervical membrane is entire.

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(*MS. received for publication* 2. III. 1925.—Ed.)

STIBAROBDELLA SUPERBA N.G. ET SP.

A NEW ICHTHYOBDELLID LEECH.

By W. HAROLD LEIGH-SHARPE, M.Sc. (Lond.).

(With 3 Text-figures.)

Habitat and Record.

Owing to the courtesy of Dr G. M. Vevers I have had the opportunity of examining a marine Ichthyobdellid leech, taken by Dr F. A. Phillipps from the cloaca of a shark, 7 feet long, caught between the islands of Aore and Santu, New Hebrides. The leech resembles *Pontobdella* superficially in being covered by warty tubercles. It possesses, however, certain peculiarities described below which justify its recognition not only as a new species but also as a representative of a new genus.

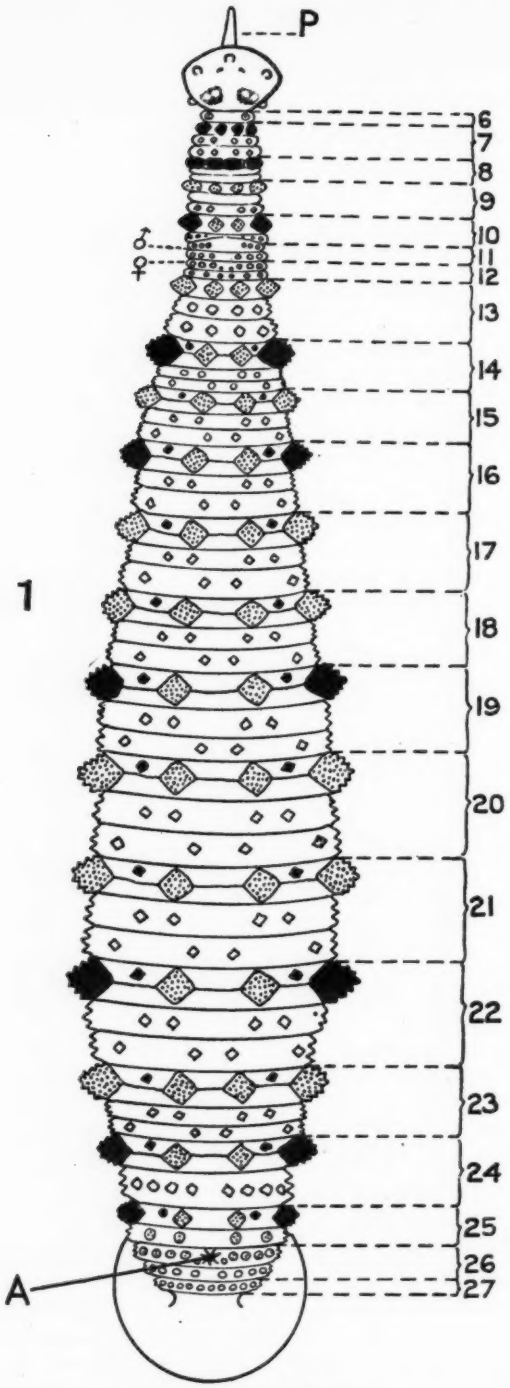
Description.

The leech is cylindrical, spindle-shaped and of a greenish-brown colour. The specimen, preserved in formalin, is 4·8 cm. long.

Suckers (Fig. 1). The *anterior sucker* is cupuliform and somewhat hood-like. It surrounds the mouth through which protrudes the proboscis. As in some species of *Pontobdella* there are externally six small spherical submarginal papillae which do not arise quite from the edge of the cup, and are almost, but not perfectly equidistant, and two more similar papillae placed toward the base of the cup, not recorded so far as I know in any species of *Pontobdella*, and here regarded as of specific importance. On the dorsal aspect of this sucker, on either side of the median line, is a black double ring-like mark having within each of the rings one hemispherical papilla, resembling the lateral and marginal ones. All the papillae referred to are translucent.

The *posterior sucker* is flattened, slightly concave, and twice the width of the anterior. Both suckers are of a translucent creamy-white appearance.

Segmentation (Fig. 1). The typical or "complete" somite is formed of three annuli. The first annulus of somites 14–24 is divided above, showing an interesting stage in ring multiplication. Annuli of this type, in which division has begun dorsally but has not yet extended to the ventral surface, are not peculiar to the leech under consideration. The anterior sucker occupies five somites. Somites 6 and 27 are uniannulate; 10–12 and 24–26 are biannulate; 7–9 and 13–23 are "complete" with three annuli. The male orifice is situated between the two annuli of somite 11; the female orifice perforates the first

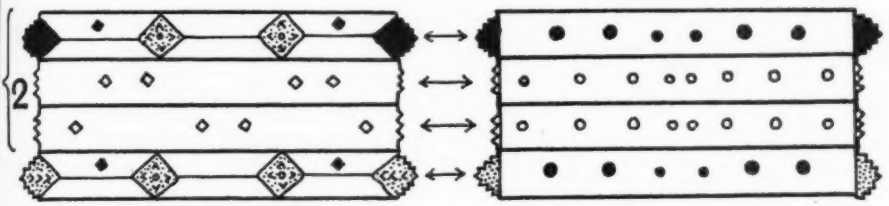


Stibarobdella superba n. sp.

Fig. 1. Entire animal in dorsal aspect. *A* = anus. Note the protruding proboscis (*P*) and the indicated positions (on the ventral surface) of the ♂ and ♀ orifices, likewise the features of the anterior sucker.

annulus of somite 12. The anus lies in the middle of the antepenultimate annulus, *i.e.* the first annulus of somite 26 (Figs. 1 and 3).

Tubercles. All the tubercles are pyramidal; from the edges of the pyramid may arise one or more pyramidal projections. The arrangement of the tubercles is indicated in Figs. 1–3. In Fig. 2 this is shown above and below in a "complete" somite in the abdominal region. Fig. 1 shows the arrangement on the dorsal surface of the whole body, and the modified arrangement on the ventral surface, in the neighbourhood of the genital orifices, is seen in Fig. 3.



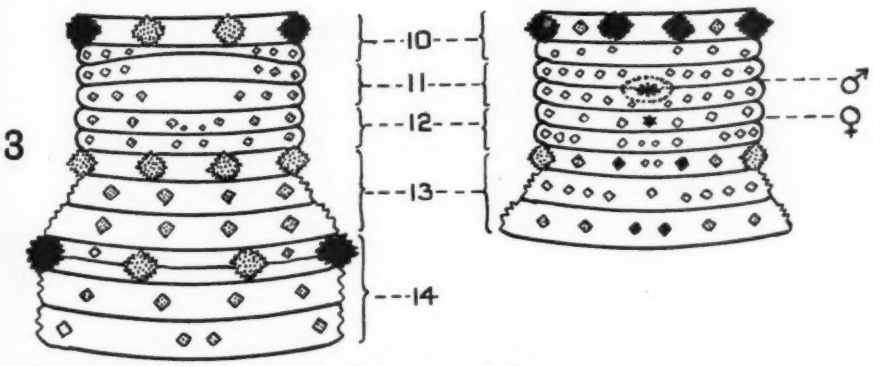


Fig. 2. A typical abdominal somite in dorsal and ventral aspects.

Fig. 3. Enlarged view of the region near the clitellum in dorsal and ventral aspects. The signs ♂ and ♀ indicate the corresponding genital orifices.

Attention is called to the conspicuous, large, or "major" tubercles (a median pair and a lateral pair) which appear in a dorsal view and occur on the first annulus of each "complete" somite and also on the first annulus of somites 10, 24 and 25. The lateral pair appear also in a ventral view; the median pair only occur ventrally on the first annulus of somite 10 (Fig. 3). Turning now to the smaller tubercles, some of these are smaller than others. These smallest tubercles are further distinguished by the absence of pyramidal projections on their edges. A pair of these occur on the dorsal surface in the upper part of the first annuli of somites 14–25. Most of the tubercles are of the same colour as the body, but some are bright grass green (indicated by black

in Figs. 1–3). It will be noticed that the two lateral series of tubercles are not all green but that some are of the same colour as the body. In the abdominal region of the body the annuli which do not bear single large lateral tubercles bear a lateral fringe of three very small tubercles.

Generic Diagnosis.

Genus *Stibarobdella*. Marine leeches resembling *Pontobdella* in being covered by conspicuous warty tubercles. The tubercles are pyramidal in form. Body divided into two regions, a short anterior "neck" and a large posterior "abdomen." Complete somite formed of three annuli of which the first is divided above in the abdominal region. No eyes.

Type species: *S. superba*, as described above. The type is deposited in the British Museum (Natural History), London.

(*MS. received for publication* 12. iv. 1925.—Ed.)

NEW RECORDS OF *BERTIELLA SATYRI* (CESTODA) IN MAN AND APES.

By ASA C. CHANDLER, Ph.D.

(*From Hookworm Research Department, financed by Indian Jute Mills Association, Calcutta School of Tropical Medicine.*)

(With 2 Text-figures.)

Bertiella satyri, normally apparently a parasite of apes, has hitherto been recorded from the orang-utan, *Simia satyri*, in Borneo, and once from a child in Mauritius.

The single human case was recorded by Blanchard (1913) from some fragments of a worm sent to him by Dr Barbeau. The fragments were obtained from the stool of a girl of eight years of age at Port Louis, Mauritius, and consisted of six pieces, including the previously unknown neck and head, amounting in all to a length of about 115 mm. Blanchard estimates that the complete worm would have measured at least 50 cm. Unfortunately Blanchard's original article is not available to me, and I have to depend on a brief review in the *Trop. Dis. Bull.* (1913).

In June, 1924, I obtained a specimen which I believe to be of the same species from a gibbon, *Hylobates hoolock*, which died in the Calcutta Zoological Gardens. This worm had a total length of about 270 mm. after being allowed to relax in water, with a maximum width of 18 mm. The head was distinctly set off from the neck, though not conspicuous, and there was an unsegmented neck about 1·5 mm. in length. Unfortunately the inconspicuous head broke off from the neck piece during the process of preparation for study and was lost. It had previously been observed, however, that the head had a diameter of about 400μ, possessed no rostellum, and had large oval unpigmented suckers which were set on the dorsal and ventral sides of the scolex, and faced laterally rather than anteriorly.

On March 12th, 1925, a piece of a tapeworm which had been passed by a female Hindu child was brought to me for examination, and proved to be a specimen of *Bertiella*. The child was two years of age, had lived in Bengal or Behar all her life, and had never eaten meat of any kind. The piece of tapeworm passed was very active and by contraction and expansion could vary its length from about 12 mm. to over 20 mm. It consisted of 21 segments which, in a partially contracted state, had a maximum diameter of about 11 mm. Inasmuch as the child was suffering from an attack of influenza, treatment was delayed until March 21st, the stools meanwhile being watched

for other pieces of the worm. During the intervening nine days five fragments of the worm were said to have been passed, although through a misunderstanding only one of them was saved. This piece also consisted of 21 segments; since it had been put into formalin while still alive it was very strongly contracted, especially in the middle portions of the proglottids, resulting in its being deeply concave at each end and strongly convex on each side. In this contracted condition it had a thickness of 3 mm. According to the parents of the child the other pieces passed were for the most part slightly longer, approaching an inch in length. The parents are quite certain that no similar pieces had been passed by the child previous to the first one submitted for examination. It is evident, as Beddard (1911) surmised, after having found a similar piece of *B. cercopitheci* broken off from the rest of the worm in the intestine of a monkey, that the segments are shed in groups, usually aggregating from one-half to one inch in length.

On March 21st the child was admitted to the Carmichael Hospital for Tropical Diseases for tapeworm treatment. She had been kept on a liquid diet for two days, and was given a dose of magnesium sulphate on the evening of admission. After her bowels had moved in the morning, about 6 a.m., a relatively large dose of filmaron was given, followed by magnesium sulphate two hours and again four hours later. A stool was passed about 8 a.m. which contained no part of the worm. Unfortunately, in spite of the double dose of salts, no other stool was passed until after 4 p.m. This stool contained the entire worm, dead, including the head, but parts of it were not in a good state of preservation due to the long retention in the bowels. The segments on the posterior portion of the worm tended to separate from each other and to curl up in a very characteristic fashion.

The total length of the worm was about 275 mm. Owing to its complete relaxation the maximum breadth was not as great as that of the less completely relaxed living segments which had been previously passed, and did not exceed 10 mm. The thickness of the largest segments was little over 1·5 mm., whereas their length was slightly more than 1 mm. In the review of Blanchard's study of the human specimen from Mauritius no mention is made of whether the worm was expelled dead or alive, or of its state of contraction. It is probable, however, that the worm was not completely relaxed when preserved, since in the terminal fragment of 15 mm. in length there were 26 segments, giving a mean length of only 577μ per segment. In the strongly contracted fragment of my worm which was put alive into formalin, the length of the segments averages even less than 500μ.

The head, as in the specimen from *Hylobates hoolock*, is distinctly set off from the neck and is very nearly spherical, though slightly flattened anteriorly. The cuticle in one anterior corner is broken and disintegration has commenced. At the anterior end there is a small knob-like projection which may be interpreted as a rudimentary rostellum, but it is possible that it is merely an artifact. The diameter of the head is approximately 475μ. The suckers

are large and oval, having a long diameter of about 220μ and a short diameter of about 150μ. The neck is about 275μ broad immediately behind the scolex, but narrows to about 225μ. Segmentation begins about 2 mm. behind the head. From the beginning of segmentation, where the strobila is only 225μ broad, the breadth steadily increases to a maximum of about 11 mm.

The excretory canals in mature segments lie about $\frac{1}{10}$ to $\frac{1}{12}$ the breadth of the segment from the margins. The dorsal canal is slightly undulant and lies straight dorsal or slightly lateral to the ventral one. The genital pores are irregularly alternate, very small, and situated near the middle of the margins of the segments.

The testes are about 75 in number on the aporal side of the ovary, while there are about a dozen on the poral side. As in other species of *Bertiella* they are situated dorsally along the anterior border of the segment, extending from one pair of excretory vessels to the other. For the greater part of this distance they are not in more than two rows antero-posteriorly, but towards the aporal side of the segment the testicular region becomes broader, and the testes may be as many as four deep. They are about 65 to 70μ in diameter.

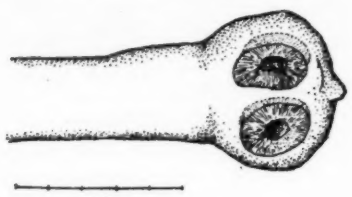


Fig. 1. *Bertiella satyri.*

The cirrus is about 310μ in length and has a maximum diameter of about 95μ; it does not reach to the excretory vessels, and the cirrus pouch is very inconspicuous. In the specimen from *Hylobates hoolock* the cirrus and cirrus pouch have a somewhat different appearance. The cirrus pouch contains a narrow duct which enlarges to form a conspicuous round sac or seminal vesicle inside of it, and the inner end of the pouch reaches to the excretory vessels. In the human worm the straight vas deferens, lying just anterior to the vagina, can be traced as far as the poral border of the ovary; it crosses the sac-like enlargement of the vagina dorsally. The ovary is crescentic and does not show a distinctly bilobed character with a connecting bridge in any of the segments; in segments in which it is fully developed it consists of club-shaped lobules which extend dorsally, laterally and medially from the common centre. When fully developed it occupies slightly more than one-fourth of the breadth of the segment; its poral margin is about one-fifth the width of the segment from the poral margin, so that the entire ovary lies well within the poral half of the segment. Lying posterior to the middle portion of the ovary is the yolk gland, which is distinctly bilobed; between its two

lobes, and slightly dorsal to it, is the shell gland. The uterus appears first as a nearly straight transverse tube extending towards the aporal margin of the segment from the region between the ovary and yolk glands, and just posterior to the testes. The extension on the poral side seems to develop later. As it grows it pushes aside the lobes of the ovary in such a way as to cut off some of the lateral lobes and push them posteriorly. Very soon after its extension across the segment the uterus begins to develop bulges, which later become pockets, on both anterior and posterior sides, but always larger on the posterior side on account of the greater space available. The vagina is complicated in structure similar to that described by Beddard (1911) for *B. cercopitheci*. It opens into a shallow genital cloaca immediately behind the cirrus; as a loosely coiled tube it passes medially behind the cirrus, being surrounded by a mass of deep-staining tissue which extends medially as far as the inner end of the cirrus. It then continues as a straight narrow tube

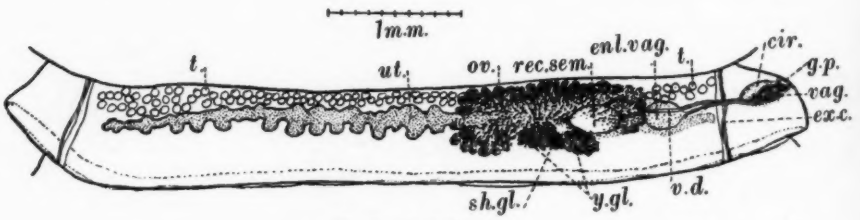


Fig. 2. *Bertiella satyri.*

which abruptly widens out into a thin-walled sac about 300μ long and 200μ wide. This abruptly narrows again into a slender tube not over 200μ long which then abruptly enters the large oval receptaculum seminis, which is about 360μ long and about 220μ broad. This organ, as it develops and fills with sperms, interferes with the ovarian lobules on the poral side just as the uterus does on the aporal side, pushing some of the lobules laterally (Fig. 2).

As the segments ripen the uterus usurps more and more space, but the testes remain in evidence for a long time, and the receptaculum seminis continues to be a very conspicuous organ. The peripheral portions of the uterus enlarge first, forming coarsely lobulated club-like ends. The more median portions of the uterus develop later, so that ultimately the uterus occupies nearly the whole segment.

The eggs correspond very closely to the description and figures given by Blanchard. They measure from 46 to 49μ in diameter, and even in perfectly fresh living eggs the outer shell is more or less crinkled; the middle envelope is very delicate. The embryo with its thick unstriated inner shell measures from 17·5 to 19μ in diameter. This inner shell is developed into a conspicuous pyriform apparatus at one pole, its elevation amounting to about 11 to 12μ. The distance from the opposite pole of the inner shell to the tip of the pyriform apparatus, which has straight closely-applied horns, is about 28 to 30μ. The

eggs in the worm from the gibbon are slightly smaller, measuring from 42 to 46μ in diameter, whereas the embryo is only 14μ in diameter, and the distance from the opposite side of the inner shell to tip of pyriform apparatus is from 22 to 26μ.

Although the measurements of the human parasite here described do not coincide exactly with those given by Blanchard (1891 and 1913), this seems to be readily explicable on account of the great variation due to the state of contraction. In all important anatomical details, so far as I have been able to compare them, they are similar, and there seems to be no reason to doubt but that we are dealing with *B. satyri* and not with one of the other species of *Bertiella* which have been described from Indian Primates.

Up to the present time six species of *Bertiella* have been described from Primates. The following key may be of use, not only in identifying specimens, but also in bringing out the morphological characters in which the species differ:

1 (8)	Eggs without pyriform apparatus	2
2 (5)	Head pigmented, especially around edges of suckers	3
3 (4)	Neck absent and head narrower than succeeding part of body; suckers directed forwards; vagina enters receptaculum seminis abruptly; ovary distinctly bilobed; genital ducts pass dorsad to both excretory canals and nerve cords; size 150 × 10 mm.; host, *Cercopithecus callitrichus*, Africa	*cercopitheci*
4 (3)	Neck present; suckers directed laterally; vagina enters receptaculum seminis by gradual enlargement; ovary less distinctly bilobed; genital ducts pass dorsally to excretory canals, but ventrally to dorsal nerve cord; size 140 × 8 to 10 mm.; host *Alouatta caraya*, Paraguay	*mucronata*
5 (2)	Head unpigmented; neck present	6
6 (7)	Suckers directed laterally; vagina enters receptaculum seminis abruptly; testes dorsal in position; size 84 × 6·5 mm.; host *Macacus sinicus*, India . . .	*conferta*
7 (6) ...	Suckers directed forwards; vagina enters receptaculum seminis by gradual enlargement; testes numerous, oval, 180 × 130μ, extending through parenchyma from dorsal to ventral side; size 515 × 13·5 mm.; host, *Macacus cynomolgus*, India	*polyorchis*
8 (1)	Eggs with pyriform apparatus; parasitic in apes and man	9
9 (10)	Neck very short, about 0·3 mm. long, as broad as head; genital pores regularly alternate; testes 300 to 400; receptaculum seminis little developed; size 130 × 15 mm.; host, *Troglodytes pan* (chimpanzee), Africa	*studeri*
10 (9)	Neck very long, 1 to 2 mm. in length, narrower than head; genital pores irregularly alternate; testes about 100 or less; receptaculum seminis well developed; size 250 to 300 or more × 10 to 12 mm.; hosts *Simia satyri*, Borneo; *Hylobates hoolock*, India; and man, Mauritius and India	*satyri*

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(*MS. received for publication* 29. VI. 1925.—Ed.)

THE SPECIES OF *STRONGYLOIDES* (NEMATODA).

By ASA C. CHANDLER, Ph.D.

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(With 2 Text-figures.)

There has been much difference of opinion as to the specificity of *Strongyloides* in different hosts, therefore an opportunity has been made use of to compare representatives of this genus, in various stages of their life histories, from monkeys, cats and man, and to compare these with the published characteristics of other forms.

Hung See Lu and Höppli (1923) have reviewed the situation as regards the species of *Strongyloides*. They accept Ransom's (1911) conclusion that *S. papillosus* and *S. longus* are identical. They also consider it doubtful whether *S. ovocinctus* from Antilocapra, considered by Ransom (1911) as a distinct species, can be so regarded. *S. suis* of pigs is considered by von Linstow (1905) as identical with *longus* (= *papillosus*), but this form has not been studied thoroughly enough to warrant a conclusion on this point. Hung See Lu and Höppli describe, with series of measurements of different stages, a species found in two macaques which died in Hamburg, and think it probable that this form also is referable to *S. papillosus* of sheep and rodents. They point out, however, that the monkey parasite is smaller and has a relatively shorter oesophagus, and if these differences proved to be constant on examination of a larger series of individuals, they suggest the name *S. simiae* for the monkey parasite. *S. stercoralis* (= *intestinalis*) of man differs from the above forms in its smaller size, number of lips surrounding the mouth, more anterior position of the vulva, shape of the tail, and in the fact that the eggs as a rule hatch before leaving the body of the host. *S. fülleborni*, described by von Linstow from the chimpanzee and a baboon in Africa in 1905, closely resembles the form described from macaques except that it is said to have a smooth unstriated cuticle. No other valid difference seems to be present and it is doubtful whether the form found in macaques is really distinct. In this case *S. simiae* becomes a synonym of *S. fülleborni*. Darling (1911) described *S. cebus* from *Cebus hypoleucus* in Panama. This species again, except for small differences in measurements, and in having "a smooth skin," closely resembles the other forms described from monkeys. Another species, *S. nasua*, described by Darling (1911) from *Nasua nasica*, differs in its smaller size and in having very prominent vulval lips in the females of the free-living generation.

Another *Strongyloides* was found by Fülleborn (1914) in a Chinese dog. This species morphologically resembles *S. stercoralis* very closely and was considered by Fülleborn as identical with the human species. Fülleborn, in fact, succeeded in producing infection experimentally in dogs in Europe by means of larvae derived from a human case. In this instance, however, the infections died out very shortly and did not become chronic as in the case of the naturally infected Chinese dog. Brumpt (1922), however, considering the discordance in geographic distribution, the difficulty in infecting dogs with *S. stercoralis*, and the fact that the dog parasite always develops heterogonically in culture, prefers to regard it as a distinct species which he calls *S. canis*.

In the course of parasitological examinations of monkeys and cats in Calcutta, I have found that almost if not quite 100 per cent. of the laboratory monkeys, *Macacus rhesus*, and a high percentage of hoolocks (*Hylobates hoolock*) which died in the Calcutta Zoological Gardens, harbour *Strongyloides*. Of Calcutta cats at least 20 per cent. have been found to be infected with *Strongyloides* although, so far as I am aware, this worm has not previously been recorded from cats.

The *Strongyloides* found in Bengal monkeys lives for the most part in the lower part of the duodenum, usually appearing first at a distance of several inches from the pyloric valve. In no case have we found embryos in the intestinal contents or in freshly passed faeces of infected monkeys; only eggs containing developed or partially developed embryos are present. The eggs measure 52 to 55μ in length by 30 to 32μ in breadth. The parthenogenetic females vary from 3 to 3·25 mm. in length, with a breadth of from 45 to 50μ, the relation of breadth to length being, therefore, about 1 : 65 to 1 : 70. The head is about 17μ in diameter. The vulva is situated from 60 to 63 per cent. of the body-length from the anterior end. The tail is short but varies in length from 42 to 56μ, being about $\frac{1}{60}$ to $\frac{1}{85}$ of the total body-length. It has a very characteristic shape, similar to that of *S. papillosus*; the body tapers a little as it approaches the anus and then is suddenly reduced just behind the anus, terminating in a short finger-like tail, broadly rounded at the tip. The oesophagus is from 820 to 870μ in length, a little more than $\frac{1}{4}$ the body-length. The mouth is surrounded by very inconspicuous lips, probably 6 in number, although it is difficult to count them. The uterus contains from 6 to 8 fully developed ova and a number of smaller undeveloped ones. The cuticle is marked by exceedingly fine striations, although superficially it appears smooth.

In cultures in soil or charcoal, development into free-living adult ma.es and females takes place within 24 hours; in some of the cultures filariform larvae appeared within 48 hours, but these were probably the offspring of the sexual forms. The females of this generation are quite variable in size and proportions, having a length of from 0·98 to 1·26 mm. with a maximum diameter in front of the vulva of from 53 to 75μ. The oesophagus has the characteristic form and varies from 143 to 182μ in length, occupying from

$\frac{1}{7}$ to $\frac{1}{8}$ of the body-length. The vulva is very prominent, the diameter through this point being from 4 to 7μ greater than the maximum diameter elsewhere. The body is slightly constricted immediately behind the vulva and then widens out again, but is never quite as wide behind the vulva as before it. The vulva varies in position from a point slightly anterior to the middle of the body-length to a point slightly posterior to it. The head is about 15μ in diameter. The uteri contain from 15 to 27 developed eggs and a mass of smaller undeveloped eggs in each uterus. The tail is slender and acutely pointed, varying in length from 125 to 153μ. The males are smaller, varying from 700 to 800μ in length with a diameter of from 36 to 42μ. The oesophagus is relatively shorter than in the females. The tail is short, curved in a sharp arc, and from

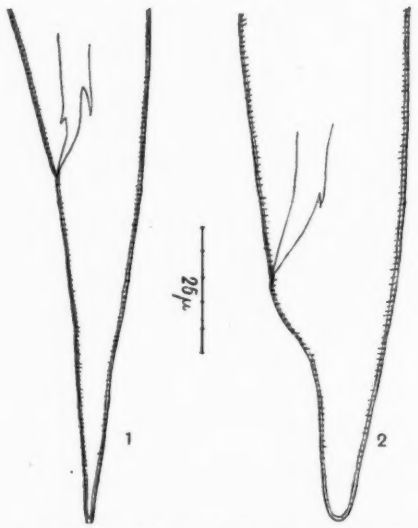

Fig. 1. Tail of *Strongyloides* from cat, typical of the shape in the *S. stercoralis* group. ×760.
Fig. 2. Tail of *Strongyloides* from *Macacus rhesus*, typical of the shape in the *S. papillosus* group. ×760.

56 to 70μ in length. There is a single pair of preanal papillae situated about 38μ in front of the anus, and a single median postanal papilla near the middle of the length of the tail. The spicules are yellowish and measure 36 to 38μ in length; the gubernaculum has the usual rhomboid shape and is about 23μ in length.

The filariform larvae vary in length from 635 to 697μ, average 656μ (25 measurements), with a diameter of 16 to 17μ, average 16·6μ. The oesophagus occupies from 43·75 to 47 per cent. of the total length, averaging 45 per cent.

This parasite of Calcutta monkeys agrees in all essential respects with that described in macaques by Hung See Lu and Höppli, except that my specimens

are a little smaller and the oesophagus relatively longer. There is no reason to believe that the two forms are not identical. Since the relatively shorter oesophagus, together with a smaller average body-length, were the only reasons suggested for the possible separation of the macaque parasites from *S. papillosus* into a new species, *S. simiae*, providing these differences proved to be constant, and since the oesophagus in my series agrees perfectly with that of *S. papillosus* and *S. fülleborni*, there appears to be no justification for the separation of the monkey parasites from *S. papillosus* except, perhaps, as a hostal variety.

The *Strongyloides* found in cats live in the upper part of the duodenum, being found with great regularity, when present at all, immediately behind the pyloric valve. Scrapings from the mucous membranes of the duodenum of infected cats invariably show swarms of embryos, but I have never seen an egg either in intestinal scrapings or in the faeces. It seems practically certain that the eggs normally hatch before being deposited, since hatched eggs are frequently seen in the parthenogenetic females. The newly-hatched embryos measure about 217 to 238μ in length.

The parthenogenetic females are from 2·6 to 2·92 mm. in length, with a diameter of from 39 to 45μ. The head is only about 14μ in diameter. The vulva is more posterior than in the monkey parasite, being 66·6 to 68 per cent. of the body-length from the anterior end. The tail is from 63 to 104μ in length, being $\frac{1}{36}$ to $\frac{1}{43}$ of the entire length, and therefore conspicuously longer than in the monkey forms. The shape is totally different. The body tapers evenly from some distance in front of the posterior loop of the uterus, and there is no sharp diminution in diameter behind the anus. The diameter at the anus is from 18 to 19μ as compared with a diameter of 28μ in the monkey parasite. Behind the anus the body tapers evenly to the tip, which is bluntly pointed. By the shape of the tail alone it is easy to distinguish the two forms even under low magnification. The mouth of the worm is surrounded by three fairly prominent lips in contrast to the larger number of inconspicuous lips in the monkey form. The oesophagus occupies about $\frac{1}{4}$ the length of the body. The uterus contains from 5 to 8 ova; those nearest the vulva are very frequently already hatched. The cuticle is finely striated.

In cultures this form develops, ordinarily at least, by the heterogonic method, producing adult males and females; in some instances the males were present in larger numbers than the females. It was observed that the males were more abundant on the first and second days of culture, whereas the females appeared to be relatively more numerous on the third and fourth days. By the fourth day no living males could be found, and on the sixth day the females had all or nearly all died. The females closely resemble those of the monkey form but were more slender, being from 1 to 1·2 mm. in length with a diameter of from 39 to 46μ. The oesophagus occupies about $\frac{1}{7}$ of the body-length. The vulva is very prominent and the body is diminished in diameter behind it; it lies near the middle of the body, but may be either

slightly anterior or posterior to it. The head is about 14μ in diameter. The uteri contain from 14 to 25 developed eggs. The tail is slender and acutely pointed, 94 to 110μ in length, and therefore relatively shorter than in the monkey form. The males are 895 to 985μ in length with a diameter of from 40 to 45μ. The length of the oesophagus has a ratio of 1 : 6·5 to the total length. The tail is from 63 to 79μ in length. There is a pair of inconspicuous preanal papillae but no median postanal papilla could be seen. The spicules are from 32 to 36μ in length and the accessory piece 21 to 22·5μ in length.

The filariform larvae are consistently smaller than those of the monkey parasite; the length varies from 525 to 615μ, with an average of 578μ, while the diameter varies from 14 to 16μ, averaging about 15μ. The oesophagus occupies from 42·2 to 47 per cent. of the body-length, averaging 44 per cent.

Cultures were made from human *S. stercoralis* at the same time and in the same way for comparison with the forms found in monkeys and cats. The free-living males and females were found to be larger than they are usually described to be. The females varied from 1·2 to 1·31 mm. in length by 60 to 63μ in diameter, and the males from 0·925 to 1·08 mm. in length by 38 to 40μ in diameter. Von Linstow (1905), quoting Perroncito, gives the size of the females as 950 by 52μ and of the males 680 by 34μ. The body of the females is somewhat narrowed behind the vulva, although von Linstow states that this is not the case. The vulva is said by von Linstow to divide the body in the proportion of 79 : 80, but my specimens showed a variation of from 15 : 17 to 27 : 26. The filariform larvae from human *Strongyloides* varied in length from 574 to 670μ with a diameter of from 16 to 17·5μ. In one culture measurements of 25 individuals showed a variation in the length of the oesophagus of from 40 to 43·7 per cent. of the body-length, averaging only 41·9 per cent., whereas in another culture from a different case it varied from 41·6 to 46 per cent., with an average of 44·6 per cent.

There can be no question, in comparing the *Strongyloides* from monkeys and cats alone, that we are dealing with quite distinct species, but the relation of these forms to others which have been described is not so certain. Reviewing all of the species, most of them seem to fall into two quite distinct groups, one of which is typified by *S. papillosus*, and the other by *S. stercoralis*.

The *S. papillosus* group may be characterised as follows: parthenogenetic females parasitic in herbivorous animals; length 3 mm. or more, usually between 3 and 4 mm. but occasionally reaching 6 mm.; mouth surrounded by more than three, probably always six, very inconspicuous papillae; body sharply constricted immediately behind the anus and ending in a short finger-like tail bluntly rounded at the tip; eggs seldom if ever hatch before leaving body of host. Female of free-living generation with tail usually more than $\frac{1}{10}$ of body-length; male (always?) with a median papilla near the middle of its length. In this group can be placed provisionally *S. papillosus*, *S. ovocinctus*, *S. fülleborni*, *S. cebus*, *S. simiae*, and in all probability *S. suis*. I have not had access to Ihle's (1918) description of *S. westeri* of horses, but

judging from its markedly larger size (8 to 9 mm.) it is quite possible that it belongs to a separate group by itself.

The *S. stercoralis* group may be characterised as follows: Parthenogenetic females parasitic in carnivorous or omnivorous hosts; length usually between 2 and 3 mm.; mouth surrounded by three fairly prominent lips; body evenly tapering from a point some distance in front of the anus and ending in an evenly tapering conical tail, bluntly pointed at the tip; eggs may hatch before or at time of oviposition, but nearly always before leaving body of host. Female of free-living generation with tail usually less than $\frac{1}{10}$ of body-length; male (always?) without a median postanal papilla. In this group can be placed *S. stercoralis*, *S. nasua*, *S. canis*, and the form here described from cats.

The combination of characters which distinguish these two groups are unquestionably of specific value. Most of the species contained within the groups, however, are doubtfully valid, since they are based largely on differences in proportionate lengths of different parts of the body, unaccompanied by other morphological differences. My own observations as well as those of many others show that there is a very wide range of variation in these ratios even in individuals from an individual host, and it is practically certain, except where very marked differences exist, or where they are accompanied by other morphological features, that they are of little value for specific diagnosis. The supposed absence of striation of the cuticle in *S. fülleborni* and *S. cebus* should be corroborated before being accepted as a valid character for the differentiation of these species. It would be a very unusual if not unique situation among nematodes if closely related members of a single genus were found to differ in the presence and absence of cuticular striation. The peculiar method of depositing eggs described by Ransom for *S. ovocinctus*, as Hung See Lu and Höppli have pointed out, is not peculiar to this form and cannot stand by itself as a valid feature for the differentiation of a species. The differences in development in culture which have been noted in various forms is also of doubtful value for specific differentiation since, as is well known, the development of a single species can be strikingly altered by environmental conditions, and it is well within the range of possibilities that the temperature or some other factor within the host may also influence the subsequent development. There is, in fact, experimental proof of this for Brumpt (1921) obtained a high percentage of free-living males, and successful heterogonous development, from culture of *S. papillosus* transferred from sheep to guinea-pigs, whereas normally *S. papillosus* of sheep produces extremely few males, and therefore only the direct development of the rhabditiform into the filariform larvae ordinarily succeeds.

That there are average differences in size and proportions between the forms found in different species of hosts appears to be quite certain, but it rarely happens that these differences do not disappear in the case of individuals. The transmission of *Strongyloides* from host to host has been accomplished in a number of instances, *e.g.*, the transfer of *S. papillosus* from sheep to guinea-

pigs by Brumpt, already mentioned, and the transfer of *S. stercoralis* from man to dogs by Fülleborn (1914). It seems reasonable to believe that we are dealing with hostal races or varieties which are the expression of environmental selections of the races contained in a hybrid animal. As the writer has previously pointed out (Chandler, 1923), most wild, *i.e.*, natural, species of animals are hybrid in composition, and a number of different lines or races differing in morphological and physiological characteristics can be isolated from them. Under a given set of environmental conditions certain ones of these races are best adapted for survival and appear to the more or less complete exclusion of other races. When the environmental conditions are altered, *e.g.*, by transference to a new species of host, and reproduction has again produced a variety of offspring, other races or lines may survive the process of natural selection, and thus give rise to the average differences in morphological and physiological characteristics observed in closely related forms in different hosts. One of the physiological characteristics involved may be adaptability to transfer to new hosts, and thus it may come about that the transfer can be accomplished only with difficulty, and in case a particular adaptable race happens to be present in the conglomeration of hybrids transferred; it is also possible that the transfer may be made from one host to another and not back again, due to the suppression, in favour of a race better adapted to the new host, of the form which was capable of development in either host, but was better adapted to the first.

Provided that constant differences in morphology or biology are demonstrable, and that the races in two different hosts are not readily interchangeable, it does not seem wise to ignore these hostal varieties, and yet one is not justified in giving them specific rank. One must either speak of *S. stercoralis* of man, of dogs, of cats, etc., or else give the races which differ from the type race trinomial varietal names, e.g. *S. stercoralis canis*, *S. s. felis*, etc. The latter system has the same advantage over the former that the binomial scientific nomenclature has over popular names, and is therefore more acceptable.

In view of these considerations it is suggested that the forms of *Strongyloides* considered in this paper be grouped into two species, *S. papillosus* and *S. stercoralis*, that the species *ovocinctus*, *fülleborni*, *suis*, *simiae* and *cebus* be reduced to hostal varieties or sub-species of *papillosus*, and that the species *nasua*, *canis*, and the form here described from cats, for which the varietal name *felis* is proposed, be made varieties or sub-species of *S. stercoralis*. Subsequent investigation may show that *fülleborni*, *cebus* and *simiae* in the first group, and *canis* and *felis*, and perhaps also *nasua*, in the second group, are synonyms. It appears evident that the morphology of the parasitic parthenogenetic females, and their biological characteristics, are more reliable for the differentiation of the various forms of *Strongyloides* than is the morphology of the free-living adults. The latter are more variable and show less marked distinguishing characters.

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(*MS. received for publication* 29. VI. 1925.—Ed.)

THE VIABILITY OF BACTERIA IN *ARGAS PERSICUS*.

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(With Plate X and 2 Text-figures.)

Introduction.

The absence of bacteria from the alimentary canal of ticks is such a constant feature that it seemed of interest to make some experiments, mainly with a view to determining the viability of various types of micro-organisms in these arthropods. It is obvious that, when sucking blood, ticks must occasionally ingest bacteria, if only septicaemic forms, and yet, with two exceptions, we have been unable to find in the literature any evidence that these micro-organisms may persist in the tick after being ingested. The two exceptions are, first, certain species of blood spirochaetes, which, as is well known, persist in some form inside the organs of the ticks responsible for their transmission; and, secondly, *Bacterium tularense*, the remarkable organism that has been shown to be transmissible by *Dermacentor andersoni*, and also by other blood-sucking invertebrates, for long periods after an infective feed. Parker, Spencer and Francis (1924), who performed experiments with ticks from the Bitter-root Valley, Montana, recovered virulent *B. tularense* from unfed *D. andersoni*, collected in nature during early spring; and as these ticks must have acquired the infection at some earlier stage, and could not have fed later than the previous summer, therefore the organisms must have survived in the tick for at least eight months. Larvae of *D. andersoni* were experimentally infected with *B. tularense* by allowing them to become engorged on infected guinea-pigs. Under laboratory conditions, these ticks were reared to the adult stage in less than three months, and in both the nymphal and adult stages infected the hosts (guinea-pigs and rabbits), on which they were placed for engorgement. In one experiment the presence of the infection was demonstrated in the ticks 247 days after feeding, and it is probable that once infected the ticks remain so for the remainder of their lives. The exact mechanism of infection is not stated, but, in view of what takes place in the transmission of *Spirochaeta duttoni* by *Ornithodorus moubata* (see Leishman (1910) and Hindle (1911)), it is of interest to note that the dried tick faeces, collected from the capsule in which six ticks had fed, when injected into a guinea-pig, produced tularaemia. This observation suggests that *Dermacentor* transmits the disease by the "contaminative" mode of infection; the organism, being present in the faeces, either enters the wound caused by the tick's bite

(or any other lesion of the skin), or is swallowed and thereby reaches the body through the wall of the alimentary canal. In these experiments with *Dermacentor*, however, the ticks were contained in brass capsules whilst feeding, so it is evident that the host could not have swallowed the faeces.

MATERIAL AND METHODS.

In the following experiments the common fowl tick, *Argas persicus*, was employed, as, owing to the kindness of Mr H. B. Johnson, Khartoum, a plentiful supply was available. This tick possesses many advantages for experimental purposes, as, with the exception of the larva, all stages feed to repletion in a comparatively short time, unlike the Ixodid ticks which require several days, and sometimes weeks, before becoming engorged.

It is well known that ticks feed by sucking the blood of vertebrates and, under normal conditions, it would be almost impossible to ensure the ingestion of micro-organisms other than those which are capable of living in the blood, such as *B. anthracis*, etc. Moreover, even in the case of such septicaemic organisms, the number in the circulation is rarely very considerable. In order to avoid any such difficulty, the ticks are fed on suspensions of bacteria in inactivated normal horse serum, employing the method originally devised by Hindle and Merriman (1912) during their experiments on the function of Haller's Organ.

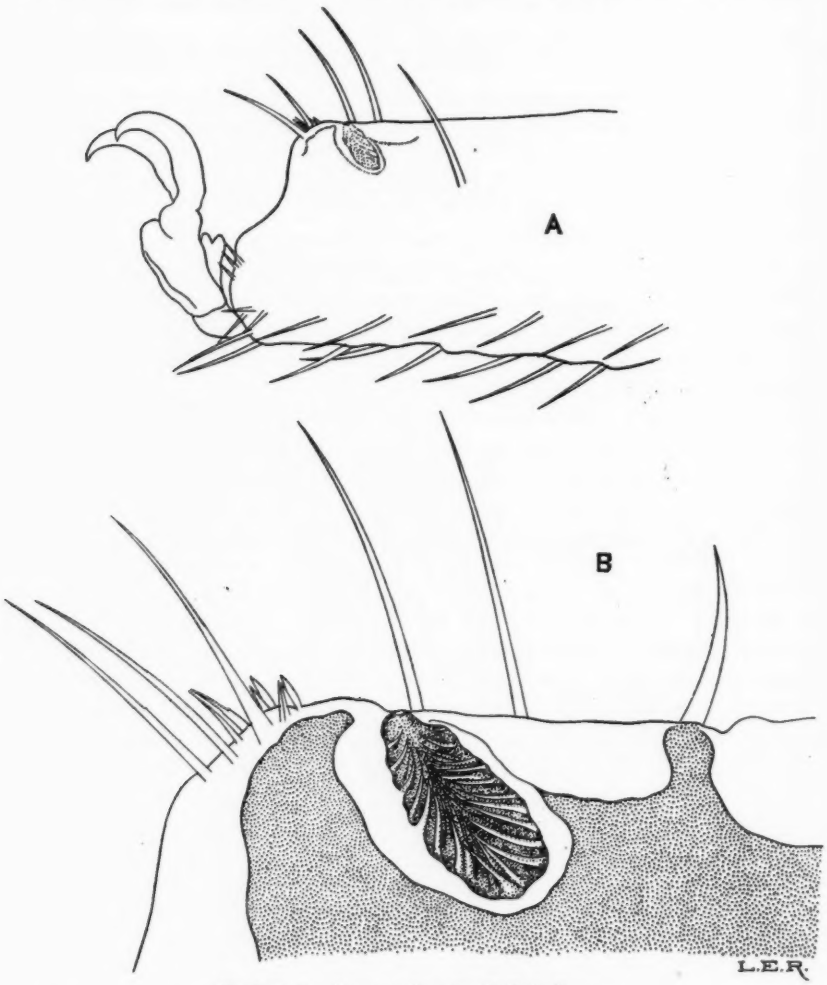
This method depends upon the fact, discovered by these authors, that the presence of Haller's organs is essential to the tick in discriminating its hosts, and that when deprived of these organs the tick is unable to distinguish between its host and any warm moist surface. Consequently it is only necessary to cut off the tarsi of the front pair of legs, in which these organs are situated, and the tick may feed on any desired liquid, so long as it is raised to approximately the temperature of the host, and covered by a suitable membrane. Text-fig. 1, (A) and (B), for which we are indebted to Dr L. E. Robinson of the Cooper Research Laboratories, shows the position of Haller's organ and also its structure.

After many trials the following procedure was found to be the most satisfactory:

A glass specimen tube three to four inches in length and one inch in diameter, was filled with metallic mercury. A shallow glass basin about one inch in diameter and provided with a flange, was fitted into the open end of the tube in such a way that its outer surface was in contact with the mercury, as shown in Text-fig. 2. The basin was fixed in position by means of a ring of plasticine under the flange. The object of this basin is to dispense with the use of large quantities of liquid, such as would have been required if Hindle and Merriman's original method had been followed. The basin was then filled with the suspension on which it was desired to feed the ticks.

In all the experiments, with one exception, the bacteria were grown on agar slopes and rich suspensions prepared by adding the growth to inactivated

normal horse serum. The only feeding surface found satisfactory was a piece of living membrane, such as the diaphragm of a guinea-pig or a rabbit, or the abdominal wall of these animals. Many attempts were made to substitute



Text-fig. 1. *Argas persicus* ♀. Haller's Organ.

A. Extremity of tarsus i, showing position of Haller's organ. Magnified 125 diameters.

B. Haller's organ in optical section, showing sensory hairs within the chamber, and the pore communicating with the exterior. Magnified 500 diameters.

non-living membranes, but without success: elastic membranes such as india-rubber and boiled sausage skin were too resistant for the ticks to penetrate; others such as parchment paper, celloidin, etc. were pierced by

the ticks, but the substance was not sufficiently elastic to close around their mouth parts, and, in consequence, the liquid oozed through the hole in the membrane and drowned them. It was found advisable to use the membrane from a freshly killed animal, and if a piece of the body wall is employed some of the muscles should be stripped off in order to render the membrane sufficiently thin to be penetrated by the mouth-parts of the tick. The piece of membrane is gently stretched by the fingers and lowered on to the open vessel containing the suspension, care being taken to avoid the formation of bubbles. The overlapping edges are then tied round the end of the tube to prevent the escape of the liquid, and also to maintain a slight tension. The tube thus prepared was then immersed in a water-bath to within a quarter of an inch of the surface of the membrane, and the bath warmed to about 45° C. and maintained at this temperature. Mercury being a good conductor of heat, the contents of the small glass basin were soon raised to a temperature slightly below that of the water in the water-bath.

Text-fig. 2. Apparatus used in the artificial feeding of ticks. The mercury is represented by the dark shading, while the small basin with its covering membrane is lightly shaded.

Ticks from which Haller's organ had been removed by cutting off the tarsi of the front pair of legs were then placed on the membrane, and, after a little hesitation, some anchored themselves and proceeded to become engorged on the fluid contained in the glass vessel. It was found advisable to cut off the tarsi two or three days before the ticks were required to feed, in order to enable them to recover from the effects of the operation. After feeding on the suspension, the ticks were removed and placed in sterile specimen tubes, each containing a strip of filter paper, and kept at a temperature of 35° C.

In the experimental feeding, cultures of the following pathogenic micro-organisms were used: *Bacillus anthracis*, *B. pestis*, *B. melitensis* var. *abortus*, *B. typhosus*, *Staphylococcus pyogenes* var. *aureus* and *Leptospira ictero haemorrhagiae*. These were all recently isolated and fully virulent strains. In addition, the following non-pathogenic bacteria were used: *Bacillus prodigiosus*, *B. mycoides*, *B. subtilis* and *Streptococcus faecalis*. The feeding was carried out in the manner described above, and, when the ticks had fed, a culture was made from the bacterial suspension in the vessel to ascertain if the organisms were still viable after exposure to the temperature necessary to induce feeding. After feeding, the ticks were isolated in numbered tubes and observed individually.

Faeces were passed at variable intervals, and occasionally it was necessary

to feed the ticks on a natural host to induce defaecation. The faeces, deposited on the strips of filter paper in the tubes, were sown on agar and in broth. Of course, only the solid residue was available, the liquid portion having been absorbed by the bibulous paper. The stomach contents of ticks which either died or were killed purposely, and the coelomic fluid obtained by cutting off one or more legs, were sown on culture media in a similar manner.

The results of feeding ticks on the bacterial cultures were as follows:

B. typhosus: Eleven ticks, in two batches, were fed on a fresh culture. Defaecation occurred eleven times between the first day and the fifty-first day following feeding, but in no case was *B. typhosus* recovered from the faeces, although, in some ticks, it was found to be still present in the stomach several days after defaecation.

From the stomach contents of six ticks which died, or were killed, between the sixth and twenty-second days after feeding, *B. typhosus* was recovered, but the examination of the five ticks remaining, killed at intervals from the thirtieth to the fifty-first day, gave negative results.

The coelomic fluid was examined on the second day and found to be sterile. From this it appears that *B. typhosus* may live in the stomach of the tick for upwards of twenty-two days, but it does not invade the haemocoele, nor is it passed living in the faeces. A control culture kept at 37° C. on the inactivated horse serum used in these experiments, was still living on the fiftieth day, showing that the eventual disappearance of the bacillus from the tick's stomach was not due to the action of this serum.

B. anthracis: Fifteen ticks in three batches were fed. Faeces passed during the first five days after feeding were sterile, but in all faeces subsequently passed up to the one hundredth day, the last occasion on which they were passed, *B. anthracis* was present. The culture from the last examination was found to have sustained no diminution in virulence or pathogenicity from its sojourn in the tick. The stomach contents, examined on several occasions between the fourth and thirty-second days, always yielded a pure culture of the bacillus. The coelomic fluid was examined on the seventh and fourteenth days and found to be sterile.

B. anthracis, therefore, not only persists in the tick indefinitely, but is also passed in the faeces. It seems to remain confined to the alimentary tract.

To test the efficiency of *A. persicus* as a possible vector of anthrax, several ticks harbouring the bacillus were fed on a guinea-pig, an animal extremely susceptible to cuti-infection with this organism. No infection, however, resulted. The mechanism of *B. pestis* infection in the case of the flea vector does not apply to the case of the tick, in which obstruction of the gut, with consequent regurgitation when feeding, does not occur. The coxal secretion, which is the vehicle of the virus in the case of spirochaetal infections, was, presumably, sterile in this case, as the coelomic fluid from which it is secreted was sterile. Infection by contamination of the puncture wound with faeces passed while feeding is conceivable, but would necessarily be of very rare

occurrence. Ingestion of the tick by its host might also lead to the infection of the latter, if it were a susceptible animal.

Staphylococcus pyogenes var. *aureus* was chosen because it is a serophyte, that is an organism capable of growing in certain sera which are inhibitory or lytic to certain other micro-organisms, such as *B. typhosus*. Seven ticks were fed on a fresh culture of a recently isolated strain, but although the faeces were examined on six occasions between the fifth and fourteenth days, and the stomach contents seven times at intervals from the eighteenth to the thirty-sixth day, the staphylococcus was never recovered. The control culture on horse serum was still living on the fiftieth day.

B. mycoides: This spore-bearing organism was employed because it was thought that *B. anthracis* might owe its survival in the tick to the formation of resistant spores. Nineteen ticks, in two batches, were fed on a culture of *B. mycoides* rich in spores, and all died within a few days of feeding. No faeces were passed but the organism was recovered from the dead ticks. The cause of the death of these ticks is not clear: The bacillus did not multiply within the alimentary canal, it did not invade the haemocoele, and it does not appear to elaborate any toxic principle inimical to the tick, for other ticks fed on filtrates of seven days old *B. mycoides* cultures on horse serum, suffered no ill effect. A third batch of four ticks was fed on a culture of the same strain of *B. mycoides*. These survived and the faeces of two were examined on the sixteenth and seventeenth days, and the stomach contents on the seventeenth and twenty-third days, but the bacillus was not recovered. It appears therefore that this organism does not persist within the tick like *B. anthracis*, and it may be assumed as probable that *B. anthracis* does not owe its survival to the formation of spores alone. *B. mycoides* grew well in the control serum culture and was still living on the fiftieth day.

B. pestis: Fourteen ticks, in three batches, were fed on a virulent strain of this organism. The faeces were examined fourteen times between the first day and the twenty-fifth day, always with negative result. The stomach contents of a tick killed on the fourth day contained the organism, but those of another tick, killed after a similar interval, and of ten others killed and examined at various times up to the thirty-sixth day, were negative. This suggests that *B. pestis* does not survive in the tick, but it should be mentioned that the life of the control cultures on serum, put up with the different batches, was short; two on horse serum died out on the twelfth and fourteenth days respectively, and one on fresh inactivated rabbit serum lived for only seventeen days.

B. melitensis var. *abortus*: A strain recently isolated from a case of undulant fever. Five ticks were fed. Faeces were examined eleven times between the second and forty-fourth days but the organism was not recovered. It was, however, recovered from the *stomach contents* of three ticks which were killed on the fifteenth and sixteenth days, although each of these ticks had passed sterile faeces within three days of death. The two ticks remaining were killed

on the forty-first and sixty-third days and the stomach contents found to be negative. The full duration of viability within the tick has not been shown, but it is not less than sixteen days. The organism is not passed in the faeces. The control culture on horse serum died out on the twenty-second day, and, therefore, it cannot be assumed that the eventual disappearance of the organism from the tick is due entirely to factors resident in the tick.

Streptococcus: During the course of the preceding feeding experiments, a contaminating streptococcus was found to be present in some individuals of two batches of ticks which had been fed on different cultures, but through membranes obtained from the same rabbit. The source of the streptococcus was traced to the rabbit. It was noticed that this contaminating organism not only persisted for a long time in the ticks but also appeared in their faeces.

A pure culture was prepared and used to feed three ticks. As in the accidental "infection," the coccus appeared constantly in the faeces, and was still present on the thirty-sixth day, the last time faeces were examined.

This streptococcus was not haemolytic, nor bile-soluble, nor pathogenic to mice, and it gave the fermentation and other reactions of *S. faecalis*.

B. prodigiosus: Of sixteen ticks, in two batches, fed on cultures of this bacillus, all except one died on the day after feeding. The survivor was killed fourteen days later but its stomach-contents were sterile. Three further attempts to feed ticks on cultures of this organism were unsuccessful.

A control culture on horse serum was still living after fifty days.

B. subtilis: This spore-bearing bacillus was employed late in the course of the work. Six ticks were fed, and, as none had defaecated during the first two weeks, they were regorged on a fowl. Three defaecated immediately after this second feed, and from the faeces of two *B. subtilis* was recovered. Further observations were prevented by the destruction of the ticks through the accidental overheating of the incubator. *B. subtilis* therefore survives in the stomach for a time, and is passed in the faeces, thus behaving similarly to *B. anthracis*.

Leptospira icterohaemorrhagiae: A virulent strain isolated by Buchanan from the Lothian Mines, and killing guinea-pigs in four to five days, was kindly supplied by Dr Okell of the Wellcome Physiological Research Laboratories. Six *Argas* were fed on the liquid from a culture of this strain on Wenyon-Noguchi medium which contained numerous actively motile *Leptospira*.

The coelomic fluid of two ticks was examined by dark ground illumination three hours after feeding, but no *Leptospira* seen. On the other hand, the stomach contents of both these individuals showed the presence of active *Leptospira*, but they were agglutinating and obviously unhealthy. After an interval of twenty hours two other ticks were examined; the coelomic fluid was negative as before, and also the stomach contents of one individual, but the other still contained a few motile *Leptospira*. After forty-six hours no trace of these organisms could be found in the tick, and moreover, the inocu-

lation of the stomach contents into a guinea-pig gave negative results. It is evident, therefore, that this organism rapidly dies out after being ingested by *Argas persicus*, a result which agrees with previous observations on the non-persistence of *Leptospra icterohaemorrhagiae* in the alimentary canal of Arthropods.

From the results detailed above, it will be seen that certain bacterial types may die out quickly in the alimentary canal of *A. persicus*; this has been demonstrated in the case of *Staphylococcus aureus*, *B. pestis* and *B. mycoides*. *B. typhosus* survived at least three weeks and *B. melitensis* not less than sixteen days. Ticks fed on *B. typhosus* and *B. melitensis* passed sterile faeces two weeks after feeding, although the micro-organisms were still present in the stomach. The cause of the failure of these bacteria to survive passage through the rectum is not apparent: it was not possible to examine the secretions of the rectum and malpighian tubules, but, as will be shown below, watery extracts of these tissues were not inimical to the life and growth of the micro-organisms.

B. anthracis, *B. subtilis* and *S. faecalis* survived in the stomach a relatively long time and were the only organisms passed living in the faeces.

It may be mentioned that during the course of these experiments the coelomic fluid was examined on ten occasions and invariably found to be sterile, the faeces were sterile in fifty examinations and the stomach contents in thirty-five, with ticks previously fed on living cultures. Bacterial sterility of these materials is the common experience with normal ticks.

The reaction of the stomach contents, about *p*H 6·6 to *p*H 7·0 in the ticks examined, is not unfavourable to the growth of any of the bacteria employed.

In attempting to elucidate the factor or factors concerned in the destruction of bacteria in the alimentary canal of the tick, the following experiments were carried out:

(*a*) *To investigate bactericidal powers.* The following test liquids were employed with cultures of *B. typhosus*, *B. anthracis*, *B. mycoides* and *Staphylococcus aureus*: coelomic fluid, stomach contents and suspensions of triturated salivary glands, stomach, rectum and malpighian tubules. Stomach contents alone were used with cultures of *B. subtilis*, *B. prodigiosus*, *B. melitensis* var. *abortus*, *B. pestis* and *Streptococcus faecalis*. As undiluted stomach contents tend to form coarse clots when manipulated in capillary tubes, it was found desirable to dilute them, and, in the tests, the pooled stomach contents of several ticks were diluted with twice or thrice their volume of sterilized normal salt solution.

The technique employed was a modification of the "Wash method of Mural Implantation" described by Wright and Colebrook (1921). Very fine sterilized capillary tubes were filled to a height of about 25 mm. with a bacterial suspension standardized, by the opacity method of Brown and Kirwan (1915), to contain approximately forty millions of organisms to 1·0 c.c. A mark was then placed on the capillary at the upper limit of the liquid, and the contents

expelled by blowing out. This left a thin film of liquid adhering to the walls of the capillary, which contained a sufficient dose of bacteria for the test. The capillary was then charged with a slightly larger volume of the test liquid, the ends were sealed in the flame and the tube incubated at 37° C. for twenty-four hours. After incubation the capillary was fitted to a teat pipette and the contents expelled, from the end opposite to that used in charging, into 1·0 c.c. of sterilized saline, 9·0 c.c. of melted agar at 50° C. added, and the mixture immediately poured as a plate culture. After twenty-four hours' incubation at 37° C. any colonies present were identified and counted. Three controls were employed as follows: (1) Substituting sterilized saline for the test liquid and plating immediately, without incubation. This gave a comparative reading of the bacterial dose employed. (2) Substituting diluted serum for the test liquid and incubating for twenty-four hours before plating. This gave an indication of the bacterial increase due to growth in a favourable medium under the conditions of the test. (3) A dose of the test liquid alone, plated after incubation to test its sterility.

These tests failed to show any bactericidal power in the various tissue suspensions and, with the exception of one doubtful result, the coelomic fluid; the stomach contents, however, were definitely bactericidal to *Staphylococcus aureus*, *B. anthracis* and *B. mycoides*. The results with *B. pestis* and *B. subtilis* were inconclusive, in the case of the latter organism chiefly owing to the difficulty of growing such an aerophile in sealed capillary tubes. *B. typhosus*, *B. prodigiosus*, *B. melitensis* var. *abortus* and *Streptococcus faecalis* were not affected; in fact for these four organisms, stomach contents behaved as a particularly favourable culture medium.

Stomach contents were strongly bactericidal to the staphylococcus, and, in several experiments, the test plates were sterile while the control plates yielded thousands of colonies.

Previous heating to a temperature of 58° C. for half-an-hour did not in any way affect the lytic power, and it is therefore clear that the lysin is not dependent on activation by alexin.

No actual measurement of the lytic value of stomach contents in the case of the staphylococcus was attempted, the tests being purely qualitative.

The destruction of *B. anthracis* was complete in some tests but in others a few colonies appeared on the plates. It is possible that these may represent more resistant individuals to the survival of which the infection of the tick is due. No attempt was made to compare the relative resistance of any such colonies with that of the parent culture.

With *B. mycoides* a few colonies appeared on the test plates, but the tests were not accepted as quite satisfactory as it was difficult to obtain a good emulsion of the organism, considerable clumping being always present.

Macroscopic tests depending upon the clearing of bacterial suspensions were impracticable owing to the great turbidity of the stomach contents and the very minute quantity available.

(*b*) *To investigate inhibitory power.* The action of faeces, stomach contents, coelomic fluid and watery extract of malpighian tubules, respectively, on the growth of *B. typhosus* and *Staphylococcus aureus* was tested in the following manner. Faeces collected from deposits on filter paper, only the dry residue being available, were rubbed up in sterile saline to make a thick suspension. The malpighian extract was prepared by triturating malpighian tubules in sterilized saline to make a milky emulsion. Each of the four test substances was then smeared over a portion of the surface of an agar slope, and, after drying, the slopes were sown with a dilution of a four hours' broth culture of the organism. The cultures were examined after twenty-four hours' incubation at 37° C. Other tests were carried out with agar plates in which faeces had been "buried" in the medium after the method employed by Fleming (1922). These plates were then spread lightly with a similar culture of *B. typhosus* to that used for the slopes, and incubated for twenty-four hours.

In no case was any inhibition of the growth of *B. typhosus* demonstrable, but in the case of *S. aureus*, although the coelomic fluid, faeces and extract of malpigian tubules were apparently inert, the stomach contents of some ticks were observed to have a very marked inhibitory action on the growth of the coccus. This is well shown in Plate X, fig. A, which illustrates the growth of the staphylococcus on an agar slope, previously prepared by smearing stomach contents in the form of a horizontal band across the middle; the position of the band is indicated by two lines on the plate. It will be noticed that the dense growth of the coccus ends off sharply at the upper and lower limits of the treated area, within which only five tiny colonies have succeeded in developing.

The tests with stomach contents were extended to include all the bacterial types used in the feeding experiments. The stomach contents of individual ticks were found to vary greatly in inhibitory power; of three separate specimens from a single batch of ticks, fed and kept under exactly similar conditions, one completely inhibited the growth of the staphylococcus, while the other two were apparently inert. It was therefore found desirable to use the pooled stomach contents from twelve to twenty ticks. With such a pool, diluted with three times its volume of sterilized saline and smeared on agar slopes as previously described, the following results were observed. There was no apparent inhibition of *B. typhosus*, *B. pestis*, *B. melitensis* var. *abortus*, *B. prodigiosus*, *S. faecalis*, *B. anthracis* or *B. mycoides*, but the growth of *B. subtilis* was completely inhibited, and that of *S. aureus* almost completely. This total inhibition of *B. subtilis* is striking in view of the entire absence of inhibition of *B. mycoides*, which even tended to grow more luxuriantly on the treated than on the untreated surface.

The inhibitory principle was not affected by exposure to a temperature of 58° C. for thirty minutes.

Plate X, figs. B and C, illustrate the inhibitory effect of diluted stomach contents on the growth of *B. subtilis*. Fig. B shows an agar plate on which

the initials "J.T.D." were written with a one in four dilution of the pooled stomach contents of twenty ticks. After drying in the incubator for thirty minutes the plate was spread with a culture of *B. subtilis*. It will be seen that no growth has occurred where the letters had been traced; the inhibitory influence has diffused slightly beyond the original lines of the letters.

The agar plate shown in Plate X, fig. C, was first sown with *B. subtilis* and thirty minutes later the letters were traced with a one in twenty dilution of a twenty-four hours' old pool of stomach contents which had been lightly sown with *B. prodigiosus*. It will be seen that the letters are formed by the growth of *B. prodigiosus* surrounded by a wider zone of inhibition of *B. subtilis*. This illustrates the resistance of *B. prodigiosus* and the susceptibility of *B. subtilis* to the action of the inhibitory principle, and also the slight diffusion of the inhibitory influence into the medium.

We are indebted to Mr A. A. Michelli of the Welcome Bureau of Scientific research for the photographs in this plate.

(*c*) *To test for phagocytosis of bacteria.* The coelomic fluid was tested with cultures of *B. typhosus* and *S. aureus*. The technique was very similar to that employed in the bactericidal tests, except that the bacterial dose was very much larger, being equivalent to about five hundred millions of organisms to 1·0 c.c. and the contents of the tubes, after incubation, were expelled on to slides, smeared out, stained and examined. Smears were made after two hours' incubation at 37° C. and again after twenty-four hours' incubation. In no case was phagocytosis of bacteria observed, but the coelomic cells were found to have taken up particles of foreign matter.

Summary and Discussion.

B. anthracis, *S. faecalis* and *B. subtilis* were found to survive, the first two indefinitely, in the alimentary canal of *Argas persicus*, and to be passed in its faeces. The stomach contents, *in vitro*, were bactericidal to *B. anthracis*, but in some of the tests a few individuals survived, and these may represent more resistant organisms, or spores, to which the infection of the tick by the relatively massive doses used in the feeding experiments was due. In smears of the stomach contents and faeces of the tick, *B. anthracis* appeared as a short thick bacillus in chains of about three to eight individuals provided with a very well-developed capsule. This capsule, not present in the agar cultures used for the bactericidal tests, may have afforded the bacillus protection within the tick. If this be true, then a very small dose of the capsulated bacilli from the blood of an infected animal might succeed in infecting the tick. A culture of *B. anthracis* recovered after one hundred days in the tick was found to be fully virulent and pathogenic.

B. subtilis seemed to behave like *B. anthracis* in the tick, but the investigation of this micro-organism was much less complete than that of *B. anthracis*. There is an apparent discrepancy between the results of the feeding experiments and the inhibitory tests *in vitro*. This might be explained by assuming

that the two ticks which harboured the bacillus to the end were deficient in the inhibitory principle, which, as shown above, is not equally active in all ticks, or by suggesting, on analogy to the bacteriophage, that the inhibitory element was completely absorbed by the large bacterial dose used in feeding, leaving an excess of bacilli to establish the infection. This might also be put forward as an alternative explanation in the case of *B. anthracis*.

All the experiments with *Streptococcus faecalis* were consistent, and showed it to be an organism wholly resistant to the bactericidal and inhibitory elements in the tick's stomach. *B. mycoides* neither survived long in the tick nor appeared in its faeces. Only four ticks however lived, and of these only two were available for examination; a number perhaps too small to justify any definite conclusion being drawn from purely negative results. Why this bacillus should have behaved differently to the other sporing bacilli, *B. anthracis* and *B. subtilis*, is not apparent. It was not more susceptible to the lytic action of stomach contents than was *B. anthracis*, and, unlike *B. subtilis*, it was wholly resistant to the inhibitory principle.

Tests with *B. pestis* and *B. melitensis* were inconclusive, as both of these micro-organisms died out soon in the inactivated horse serum used in feeding; *B. pestis* in two weeks and *B. melitensis* in about three weeks. In the case of *B. melitensis* the organism apparently survived as long in the tick as it did in the serum control. In order to obtain more conclusive results with these two organisms, it is necessary to find a medium which, while providing a suitable food for the tick, will not prove inimical to the life of the bacillus. It is noteworthy, however, that the growth of these organisms was not inhibited, and *B. melitensis* was not destroyed, *in vitro* by ticks' stomach contents.

B. typhosus presented a curious problem in that, while it survived in the stomach for at least twenty-two days, it was never recovered from the faeces; this applies also to the case of *B. melitensis*. Whether or not this is due to some factor existing in the rectum or malpighian secretion, has not been shown. The cause of the eventual disappearance of *B. typhosus* from the tick is obscure. It may be that it is killed off by the products of its own life activities in a medium particularly favourable to its growth. No lysin or inhibitory principle affecting *B. typhosus* was found in the tick.

Staphylococcus aureus furnished very conclusive results. It died out quickly after ingestion by the tick, and the evidence of the feeding experiments was fully supported by the results of the tests *in vitro* which showed the stomach contents to be powerfully bactericidal and inhibitory to the coccus.

The source and nature of the lytic and inhibitory principles require further investigation which will be made the subject of a later communication by one of us (J.T.D.). For the present, the results of the control cultures on horse serum make it clear that this medium is not the source. Other tests carried out with the inactivated blood of the fowls used for the normal feeding of the ticks gave no appreciable evidence of bactericidal or inhibitory power.

Therefore it may reasonably be assumed that the source of these elements is within the tick, but whether they are derived from the salivary glands or the stomach has not been shown. With regard to their nature, their action is not dependent upon the presence of alexin, and the lysin may be of the nature of an enzyme, or perhaps something similar to the "lysozyme" present in certain animal secretions, described by Fleming (1922). Both the lytic and inhibitory principles vary in amount in individual ticks, and neither is inactivated by exposure to a temperature of 58° C. for thirty minutes.

In all cases of ticks fed on bacterial cultures the micro-organisms remained within the confines of the alimentary canal, and no evidence of invasion of the haemocoele was found. Defaecation was the only process by which bacteria were found to leave the tick, and as only a few types were passed in this way, and defaecation occurs only at long intervals, and not as a rule during feeding, it seems very improbable that *Argas persicus* could be an efficient vector of any of the bacterial viruses employed in this work.

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EXPLANATION OF PLATE X.

Fig. A. An agar slope showing inhibition of growth of *Staphylococcus aureus* by the stomach contents of *Argas* .

Fig. B. An agar plate showing a similar inhibition of the growth of *B. subtilis*. The letters were traced with stomach contents before sowing the culture.

Fig. C. An agar plate culture illustrating the resistance of *B. prodigiosus* and the susceptibility of *B. subtilis* to the inhibitory influence of stomach contents.

(*MS. received for publication* 8. VII. 1925.—Ed.)

Fig. A.

Fig. B.

Fig. C.

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PARASITOLOGY is published about four times a year. The numbers afterwards are issued in volumes each containing four numbers.

Papers for publication should be sent to Professor GEORGE H. F. NUTTALL, F.R.S., Longfield, Madingley Road, Cambridge. Other communications should be addressed to the University Press, Cambridge.

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The subscription price is £2. 5*s*. per volume (post-free), payable in advance; single numbers 15*s*. net (double number 30*s*. net). Subscriptions may be sent to any Bookseller, or to The Cambridge University Press, Fetter Lane, London, E.C. 4.

The Cambridge University Press has appointed the University of Chicago Press agent for the sale of *Parasitology* in the United States of America and has authorised the following prices: Subscription $10.50 net per volume; single numbers $3.50 net each, double numbers $7.00 net each.

PRINTED IN GREAT BRITAIN BY W. LEWIS AT THE CAMBRIDGE UNIVERSITY PRESS